이학박사학위논문

한국의 말라리아 매개 얼룩날개모기류에 관한 계통 및 집단유전학적 연구

Phylogenetic and Population Genetic Studies on Malaria Vector Mosquito *Anopheles* Hyrcanus Group in Korea

2012년 8월

서울대학교 대학원

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강승현의 박사학위논문을 인준함

2012 년 8 월

위 원 장 (인)

부 위 원 장 (인)

위 원 (인)

위 원 (인)

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A dissertation submitted in partial fulfillment

of the requirement for the degree of

DOCTOR OF PHILOSOPHY

TO THE FACULTY OF

THE SCHOOL of BIOLOGICAL SCIENCES

at

SEOUL NATIONAL UNIVERSITY

by

SEUNGHYUN KANG

Date approved

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ABSTRACT

Phylogenetic and Population Genetic Studies on Malaria Vector Mosquito *Anopheles* Hyrcanus Group in Korea

Seunghyun Kang
School of Biological Sciences
The Graduate School
Seoul National University

With continuing population growth, global warming and climate change, countermeasures for malaria and other vector-mediated disease are urgently needed. Vector mosquitoes have different vector capacity depending on species and populations. Understanding the taxonomic status, genetic diversity, population structure, population dynamics, and geographical distribution of the vector species provides insights into dispersal potential and disease patterns. In this study, multilocus molecular markers were used to investigate phylogeny, genetic diversity, introgression, and population structure of the Korean malaria mosquito *Anopheles* Hyrcanus group. Molecular phylogeny of six Korean malaria vectors showed two well-supported clades, *Anopheles kleini* and *Anopheles belenrae* + *Anopheles sinensis* sensu stricto. The genetic introgression analysis between *An. sinensis* s.s. and *An. kleini* suggested possible gene flow from *An. sinensis* s.s. to *An. kleini*, even though they showed very high genetic differentiation and fixed polymorphisms. An insecticide resistance polymorphism study on the six Korean malaria vectors revealed that knockdown resistance mutations existed only in *An. sinensis* s.s. No mutations were found in the other five species, and furthermore, a L1014F TTC mutation was observed for the first time in the *An. sinensis* s.s. species. Population

genetic structure analysis of *An. sinensis* s.s. in East Asia based on mitochondrial control region and microsatellite suggested that the Taebaek and Sobaek Mountains that cross the Republic of Korea are significant genetic barriers in East Asia.

Keywords: malaria vector mosquitoes, Hyrcanus group, population genetic structure, phylogeny, multilocus analysis, insecticide resistance

Student identification number: 2006-22932

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ABBREVIATIONS

ROK	Republic of Korea
DMZ	Demilitarized Zone
WHO	World Health Organization
PCR	polymerase chain reaction
EPIC	exon-primed-intron crossing
NJ	neighbor joining
MP	maximum parsimony
ML	maximum likelihood
d_N/d_S	estimate of selection pressures
d_N	relative rate of nonsynonymous substitutions
d_S	relative rate of synonymous substitutions
BI	Bayesian inference
IM	isolation with migration
MCMC	Markov Chain Monte Carlo
ESS	effective sample size
NR	non-recombining block
VGSC	voltage-gated sodium channel
kdr	knockdown resistance
ITS2	internal transcribed spacer 2
HWE	Hardy-Weinberg equilibrium
LD	linkage disequilibrium
UPGMA	unweighted pair group method with arithmetic mean
θ	theta value=$4N\mu$
S	number of polymorphic sites
π	mean value of pairwise differences
AMOVA	analysis of molecular variance

N_A	mean number of alleles per locus
N_E	effective number of alleles
H_O	observed heterozygosity
H_E	expected heterozygosity
AR	allelic richness
PCA	principal component analyses

INTRODUCTION

Malaria is one of the most prevalent parasitic diseases in the world, with about 216 million cases and an estimated 655,000 deaths reported in 2010 (Organization 2011) (Figure 1). Malaria is caused by the protozoan *Plasmodium*, which is transmitted to humans by the bite of infected female *Anopheles* mosquitoes, the malaria vectors. There are four species of *Plasmodium* that cause human malaria: *Plasmodium falciparum, P. vivax, P. malariae,* and *P. ovale.* Among these four species, *P. falciparum* and *P. vivax* are responsible for the significant majority of malaria infections.

Before the 1960s, the Republic of Korea (ROK) was a *P. vivax* malaria-endemic country, and malaria prevailed throughout the country. In the late 1970s, malaria was eliminated through eradication efforts by the World Health Organization (WHO) and the government of the ROK. However, since 1993, malaria has re-emerged in the north-western region of Gyeonggi-do (Chai et al. 1994) (Figure 2), and over 1,000 cases of malaria have been diagnosed every year with a peak of 4,142 cases diagnosed in 2000 (Lee et al. 2007) (Figure 3). Although the malaria-vector mosquitoes, the *Anopheles* species, are prevalent throughout the Korean Peninsula, most of the incident cases in the ROK have been reported in the northern part of Gyeonggi-do and the north-western part of Gangwon-do near the Demilitarized Zone (DMZ) between North Korea and the ROK (Ree 2000). An area

of high transmission is found in North Korea along the DMZ as well, which suggests a parallel outbreak occurred in both countries (Han et al. 2006).

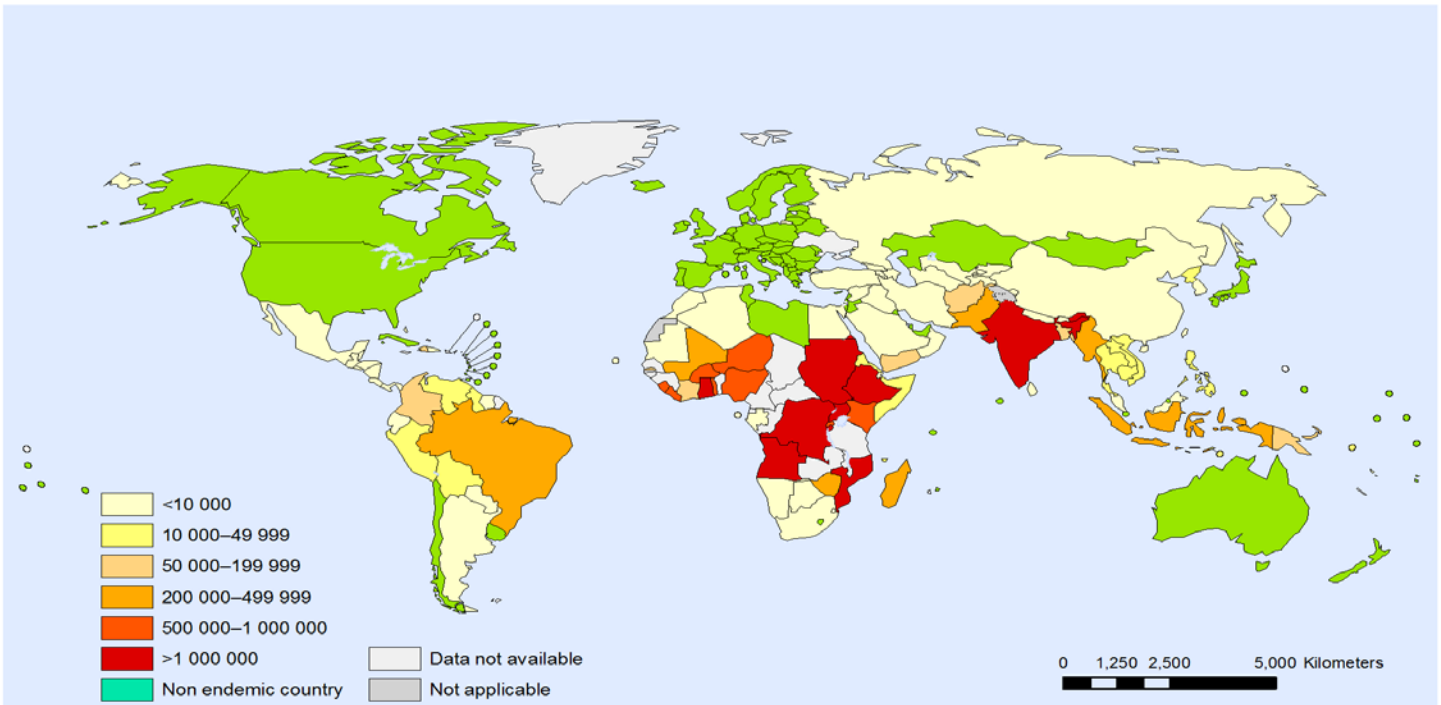

Figure 1. Number of confirmed cases of malaria reported in 2010 (Source: WHO, World Malaria Report 2011).

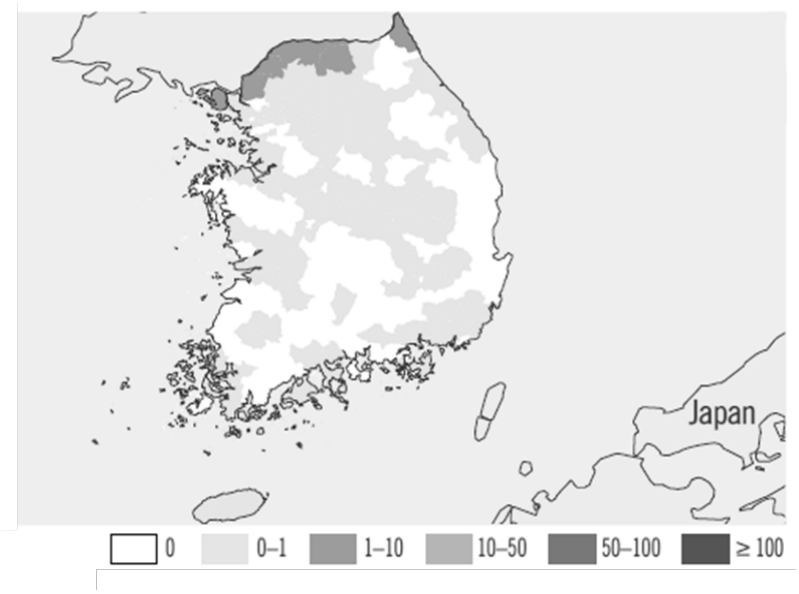

Figure 2. Distribution of confirmed malaria cases per 1,000 population in the ROK (Source: WHO, World Malaria Report 2011).

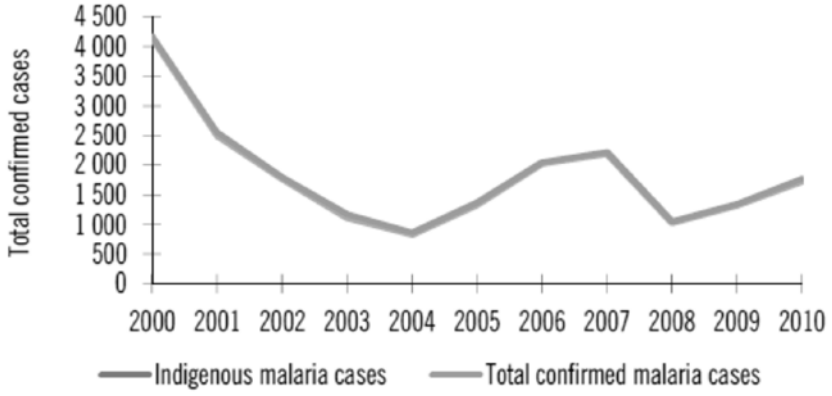

Figure 3. Number of cases of malaria reported in the ROK, 2000–2010 (Source: WHO, World Malaria Report 2011).

In the ROK, eight *Anopheles* species, including the two recently reported species of *Anopheles belenrae* and *Anopheles kleini*, have been recorded so far (Tanaka et al. 1979; Rueda 2005). These eight species belong to three groups (Hyrcanus, Barbirostris, and Lindesayi) in the subgenus *Anopheles*. The Hyrcanus group consists of 27 species, six in the Lesteri subgroup, four in the Nigerrimus subgroup, and the rest 17 unplaced species within the group (Harbach 2011). The following six of these species have been reported in the ROK: *Anopheles sinensis* sensu stricto, *Anopheles lesteri*, *Anopheles pullus*, *Anopheles sineroides*, *An. kleini*, and *An. belenrae* (Tanaka et al. 1979; Li et al. 2005; Rueda 2005; Hwang 2007). Especially, the three species, *An. sinensis* s.s., *An. kleini*, and *An. balenrae*, comprise a species complex called *An. sinensis* sensu lato. Because they occur in sympatry and it is hard to distinguish *An. belenrae* and *An. kleini* by morphology from *An. pullus* and *An. sinensis* s.s. (Ma et al. 2000; Min et al. 2002; Ree 2005; Lee et al. 2009; Shin et al. 2011). Thus, molecular methods have been used for species identification (Wilkerson et al. 2003; Li et al. 2005; Ree 2005; Joshi et al. 2009). The other two non-Hyrcanus species, *Anopheles koreicus* and *Anopheles lindesayi*, belong to the Barbirostris and Lindesayi groups, respectively (Tanaka et al. 1979).

The primary vector species for malaria in Korea has long been declared *An. sinensis* s.s. (Ree 2000; Ree 2005), but their *P. vivax* malaria susceptibilities and vectorial capacities have been controversial. Recent studies have suggested that *An. pullus*, *An. kleini*, and *An. lesteri* are the primary vector species and that *An. sinensis*

s.s. does not play a primary role (Lee et al. 2007; Joshi et al. 2009; Joshi et al. 2011). In addition, *An. sineroides* and *An. belenrae* have been reported as *P. vivax*-positive based on enzyme-linked immunosorbent assays and polymerase chain reactions (PCRs) (Coleman et al. 2002; Rueda et al. 2010).

Hybridization between related species of the anopheline species, which rarely takes place in natural environments, might complicate malaria vector control (Davidson 1964; White 1971; Temu et al. 1997; Slotman et al. 2005). Evidence of introgressive hybridization has been reported for the *Anopheles gambiae* complex (Davidson 1964; White 1971; Garcia et al. 1996; Temu et al. 1997; Weill et al. 2000; Slotman et al. 2005; Djogbénou et al. 2008). In addition, recent studies have reported the presence of natural hybrids between *An. sinensis* s.s. and *An. kleini* in the ROK (Joshi et al. 2009).

For last two centuries, management of *Anopheles* populations has been the most effective form of malaria control, but it continues to be a challenge (Catteruccia 2007; Programme 2010). Identifying population demes, lineages, or molecular forms that may have differential vectorial capacities provides insights into malaria management (Donnelly et al. 2002; Michel et al. 2005; Cohuet et al. 2010). The historical genetic exchange defines these genetic entities, and it is spatially and temporally limited (Besansky et al. 1997; Walton et al. 2001; Donnelly et al. 2002; McKeon et al. 2010). The advent of PCR and identification of a variety and number of genetic markers have facilitated a wide array of investigations in diverse fields such as molecular taxonomy, population structure, and

phylogeography. Each molecular marker represents different points in time in the historical demography of malaria vectors (Loaiza et al. 2011).

Mitochondrial DNA has been widely used for molecular taxonomy, phylogenetic relationships, and population genetic studies in malaria vectors (Norris 2002; Loaiza et al. 2011). Because of its high copy numbers and availability of conserved primers, mitochondrial DNA was ideal as a starting point to investigate genetic diversity. As mitochondrial DNA follows the molecular clock, using mitochondrial DNA markers allows calculation of time estimates (Moreno et al. 2010). Microsatellites are highly polymorphic nuclear DNA markers that can detect differentiation even in weakly structured species because of their higher mutation rate compared with mitochondrial or nuclear genes. These markers have been widely used to estimate contemporary gene flow among *Anopheles* populations including *An. gambiae, Anopheles albimanus*, and *Anopheles dirus.* Recently, multiple analyses of nuclear DNA markers have become widely applicable in phylogeography and phylogenetics (Adekambi and Drancourt, 2004; Christensen et al., 2004; Holmes et al., 2004; Naser et al., 2005; Thompson et al., 2005; Wertz et al., 2003) because genes and genomes diversify during evolution.

In this study, I investigated the phylogeny of Korean malaria mosquitoes and examined introgression and speciation between *An. sinensis* s.s. and *An. kleini* using a multilocus approach, polymorphism, and the geographical distribution of insecticide resistance genes in Korean malaria mosquitoes, along with the

population structure of *An. sinensis* s.s. based on mitochondrial DNA and microsatellites.

Chapter 1. Phylogenetic Inference of *Anopheles sinensis* Complex and Semipermeable Species Boundaries: A Multilocus Approach

Introduction

To understand evolutionary patterns among related species, reliable inference of phylogenetic relationships is crucial. However, inferring phylogenetic relationships based on a single gene is unclear because genes and genomes diversify during evolution. Especially, incomplete lineage sorting results in inconsistency between gene trees and species trees (Nei 1987; Pamilo and Nei 1988; Takahata 1989; Avise 2000). To address this, utilizing multiple genes of different functions and of both coding and non-coding regions has been recommended (Jennings and Edwards 2005; Edwards et al. 2007).

In the ROK, six malaria vectors, *An. sinensis* s.s., *An. kleini, An. lesteri, An. belenrae, An. pullus,* and *An. sineroides,* have been reported so far (Tanaka et al. 1979; Li et al. 2005; Rueda 2005; Hwang 2007) and their phylogenetic relationships have been estimated using rDNA ITS sequences (Whang et al. 2002; Li et al. 2005; Hwang 2007; Joshi et al. 2010) and mitochondrial DNA COI sequences (Park et al. 2003). *An. kleini* and *An. belenrae* were recently reported as new species separated from *An. sinensis* s.s. based on rDNA ITS2 regions (Li et al. 2005). These three species are morphologically indistinguishable and show a relatively small level of

genetic differentiation of 10.7% based on the rDNA ITS2 regions. Thus, these species are considered as *An. sinensis* complex. Importantly, a rare rate of natural hybrids between *An. kleini* and *An. sinensis* s.s., the primary and secondary malaria vectors in the ROK, respectively, have been reported (Joshi et al. 2009). However, most phylogenetic studies on *An. sinensis* complex so far have been based on ITS2. In this chapter, multilocus approaches were used to explore phylogenetic relationships among six species in the Korean Hyrcanus group especially *An. sinensis* complex and genetic polymorphism and divergence within and among *An. sinensis* s.s. and *An. kleini*.

Materials and Methods

Mosquito species collection and identification and DNA isolation

Anopheles mosquitoes were collected from five locations in the ROK and one location in Thailand (Table 1). The mosquito specimens were first identified based on their morphological characteristics under a stereomicroscope, and then confirmed by molecular identification methods using multiplex assays (Joshi et al. 2010). Genomic DNA was extracted by standard phenol extraction or DNeasy Blood and Tissue kit (QIAGEN, USA).

Table 1. Taxonomic states of *Anopheles* species and details of collection sites.

Species	Location of samples	N	Geographical coordinates
Anopheles sinensis	YEONCHEON	16	38° 08′ 00″ N 127° 06′ 00″ E
	GURYONGPO	2	35° 58′ 21″ N 129° 33′ 04″ E
	THAILAND	2	UNKNOWN
Anopheles belenrae	PAJOO	3	37° 46′ 00″ N 126° 47′ 00″ E
Anopheles kleini	PYEONGCHANG	3	37° 21′ 32″ N 128° 22′ 26″ E
	YEONCHEON	14	38° 08′ 00″ N 127° 06′ 00″ E
Anopheles lesteri	PAJOO	4	37° 46′ 00″ N 126° 47′ 00″ E
Anopheles pullus	YEONCHEON	4	38° 08′ 00″ N 127° 06′ 00″ E
Anopheles sineroides	SORAE	1	37° 23′ 00″ N 126° 43′ 00″ E

Multilocus primer design and DNA sequence data retrieval

According to the finding that exons are highly conserved across diverse taxa, exon-primed-intron crossing (EPIC) (Palumbi 1996) methods were adopted to design primers. The mRNA sequences of *An. sinensis* and the whole genome sequence information of *An. gambiae* were downloaded from NCBI and ENSEMBL databases. The gene ID and accession numbers were as follows: 14-3-3ζ: FJ687751.1, DNAJ (HSP40): HM013840.1, RpL14: AgamP3:2L:24567599:24570820:1. Highly conserved exon regions across *An. sinensis* and *An. gambiae* or *Aedes aegypti* and *An. gambiae* were subject to primer

designs. In total, 16 primer pairs were designed and tested for amplification in six Korean *Anopheles* species. In this study, three DNA markers, DNAJ (HSP40), 14-3-3ζ, and RpL14, were successfully amplified in all six Korean *Anopheles* mosquito varieties, while GCSβ markers were only amplified in *An. sinensis* s.s. and *An. kleini* (Table 2). Furthermore, ITS2, COI, COII, 14-3-3ζ, DNA-J (HSP40), and RpL14 gene- homologous DNA sequences of *An. gambiae* and COI and COII homologous DNA sequences of *A. aegypti* were retrieved from NCBI for later phylogenetic analyses for calibration and out-group comparisons. The accession numbers were: *An. gambiae* (ITS2: EU104648.1; COI: DQ792578.1; COII: L20934.1; 14-3-3ζ: XM_564587.3; DNAJ (HSP40): XM_316797.4; RpL14: AgamP3:2L:24567599:24570820:1), and *A. aegypti* (COI+COII: AF425846.1)

Table 2. Details of genes and gene fragments on the basis of *An. sinensis* sequence and PCR annealing temperatures for amplification in Korean Hyrcanus species.

Gene	Gene details			Details of fragments analyzed		
	Chromosomal location *An. gambiae*	Function	Coding/non-coding part taken for analysis	Primer sequence 5'-3'	Reference	Annealing temperatures (°C)
ITS2	Nuclear genome	No function assigned yet	Non-coding	F: ATAATGTGAACTGCAGGACACATG R: GGGTTGTCACACATAACTTGAGGC	Park et al. (2003)	52-56
COI	Mitochondrial genome	Catalyzes transfer of electrons in mitochondrial electron transport chain	Coding	F: GGTCAACAAATCATAAAGATATTGG R:TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)	55
COII	Mitochondrial genome	Catalyzes transfer of electrons in mitochondrial electron transport chain	Coding	F: GATTAGTGCAATGAATTTAAGC R: GAGATCATTACTTGCTTTCAGTC	Min et al. (2002)	55
14-3-3ζ	2L	Pivotal role in cell survival, apoptosis and signal transduction	Coding+ non-coding	F: AGGCAAAATTAGCCGAACAA R: TTTGGGAATTAAGAATTTGTCCA	This study	55
DNA-J (HSP40)	2L	Protein translation, folding, unfolding, translocation, and degradation. They act primarily by stimulating the ATPase activity of Hsp70s	Coding	F: CGCAACAAAGCTCTGGAAAT R: GCTTTGTAACGGGGATTGTC	This study	55
RpL14	2L	Ribosomal protein L14	Coding + non-coding	F: TTTCTTTCCGGTCCAAGATG R: GCGTCCCTTGTATTTTCCAA	This study	50
GCSβ	X	Soluble guanylyl cyclase beta subunit (GCSbeta)	Coding + non-coding	F: TATGGCGAAGAACGTCATGATGGG R: CGAACAGGCAGTAGCGCGGCAT	Dixit et al. (2011)	55

PCR amplification and sequencing

One to 16 specimens from each species were subject to the sequencing procedure. In total, seven genes, ITS2, COI, COII, 14-3-3ζ, DNA-J (HSP40), RpL14, and GCSβ, were PCR-amplified using the primer pairs and annealing temperatures in Table 2. All PCR reactions were carried out in a total volume of 25 μL, and contained 5× *Taq* polymerase buffer, 1 mM dNTP mix, each primer, 500 mM, 2.5–250 pg total DNA, and 0.04 U/μL of go*Taq* polymerase (Promega, Madison, WI). The PCR conditions were as follows: initial denaturation at 95°C for 5 min, 35 cycles of denaturation at 95°C for 30 s, annealing at primer temperature specified in Table 2 for 30 s, elongation at 72°C for 1 min, and final extension at 72°C for 5 min. The PCR products were sequenced using both amplifying primers and a Big Dye terminator sequencing kit (Applied Biosystems) according to the manufacturer's instructions. After purification, the reaction products were analyzed on an ABI PRISM Genetic Analyzer 3100 (Applied Biosystems). Bidirectional sequences were aligned and visually examined using Sequence Navigator v1.0.1 (Perkin Elmer-Applied Biosystems). Heterozygous DNA sequences that produced double peaks in chromatograms from both directions were recorded as heterozygotes.

DNA sequence editing and alignment

Multiple sequence alignments of six genes were conducted using MEGA 5.05 (Tamura et al. 2011). Since four nuclear genes were used and some individuals showed heterozygous DNA sequences with double peaks in both directions, all of the unphased nuclear DNA sequences were reconstructed by PHASE algorithm

(Garrick et al. 2010) implemented in DnaSP v5 (Librado and Rozas 2009) before performing further analyses.

Phylogenetic tree construction

Phylogenetic trees were constructed with the seven combinations (ITS2, COI, COII, 14-3-3ζ, DNAJ (HSP40), and RpL14) following four different approaches, i.e. neighbor joining (NJ), maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). NJ trees were constructed in MEGA 5.05 using the maximum composite likelihood model for nucleotide substitution and bootstrapping. The best-fit models of nucleotide substitution for phylogenetic tree estimation with ML and BI methods were estimated using MODELTEST (Posada and Crandall 1998). Both MP and ML phylogenetic trees were constructed by PAUP 4.0b (Swofford 2000). MP analyses were performed under a heuristic search option with TBR branch swapping, random stepwise addition of sequences, and 100 pseudoreplicates for branch support. ML analyses were performed utilizing 100 pseudoreplicates, with a heuristic search, stepwise addition, and TBR branch swapping. BI was carried out using MRBAYES 3.2 (Ronquist and Huelsenbeck 2003) with default values for prior probabilities and 10,000 generations of MCMC simulations.

Species trees and estimation of divergence time using multiple DNA sequences

In order to estimate species trees from multilocus data, *BEAST analyses implemented in the BEAST v1.7.1 (Drummond and Rambaut 2007) package were

performed and all six genes were used species tree construction [input files: Appendix 1]. As the COI and COII gene trees were exactly concordant with the species trees and these genes followed the molecular clock hypothesis, both of them were used to estimate divergence times. A lognormal relaxed clock with a commonly estimated mitochondrial DNA substitution rate in insects (2.3%/Myr (Brower 1994)), a Yule speciation model, and a divergence time of 145–200 Myr between *An. gambiae* and *A. aegypti* (Krzywinski et al. 2006) were applied for the divergence time estimation with runs for 10,000,000 generations. The posterior probability density distribution and 95% confidence intervals of divergence times were obtained using TRACER v1.5 in BEAST package.

Polymorphism, recombination, and divergence analyses

The DNA sequences from seven loci of *An. sinensis* s.s. and *An. kleini* were aligned using MEGA 5.05 (Tamura et al. 2011), and population genetic analyses were performed using DnaSP v5 (Librado and Rozas 2009). The optimal recombination-filtered block was constructed using IM_{GC} (Woerner et al. 2007). Gene genealogy analyses based on NJ were performed using MEGA 5.05 with the maximum composite likelihood model for nucleotide substitution and bootstrapping.

Selection test, isolation, and introgression

An estimate of selection pressures (d_N/d_S) acting on given proteins was provided by the relative rate of nonsynonymous (d_N) and synonymous (d_S) substitutions. The d_N / d_S calculation was conducted by using KaKs CALCULATOR (Zhang et al. 2006). The parameter estimates of an Isolation with Migration (IM) model (Figure 4) based

on Markov Chain Monte Carlo (MCMC) simulations was carried out using the IM program (Nielsen and Wakeley 2001), and the Infinite Sites model for nuclear genes and the HKY model for mitochondrial genes were chosen as the mutation models for the IM simulations. Convergence was assessed through multiple independent runs (three independent MCMC runs) with burn-in of 100,000 steps, 10 chains, and effective sample size (ESS) value monitoring [input files: Appendix 2].

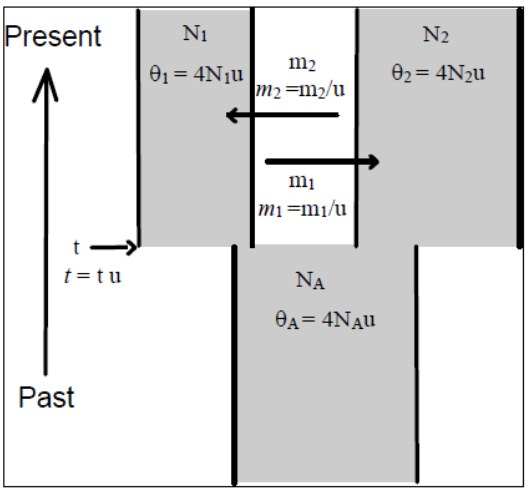

Figure 4. The isolation with migration model. N_A represents an ancestral population of effective size. N_1 and N_2 represent two descendant populations of effective size. m_1 and m_2 represent gene exchange rates after the population separation (Source: Hey and Nielsen, 2004).

Results

Phylogenetic inferences with multilocus data

Both congruent and incongruent phylogenies among genes were observed in the six *Anopheles* species. COI, COII phylogenetic trees constructed with all four different

methods were congruent, with variable bootstrap values or posterior probabilities (Figure 5), even though the lineage sorting between *An. sinensis* complex was incomplete using the COI and COII sequences (Figure 5 b and c). The gene genealogies of three genes, ITS2, 14-3-3ζ, and RpL14, supported the two clades *An. kleini and An. belenrae* + *An. sinensis* s.s. with all four of the different tree construction methods, (Figure 5 a, d, and f). Monophyly among *An. sineroides* and *An. lesteri* was observed in three gene trees (COI, COII, and DNAJ (HSP40)) (Figure 5 b, c, and f).

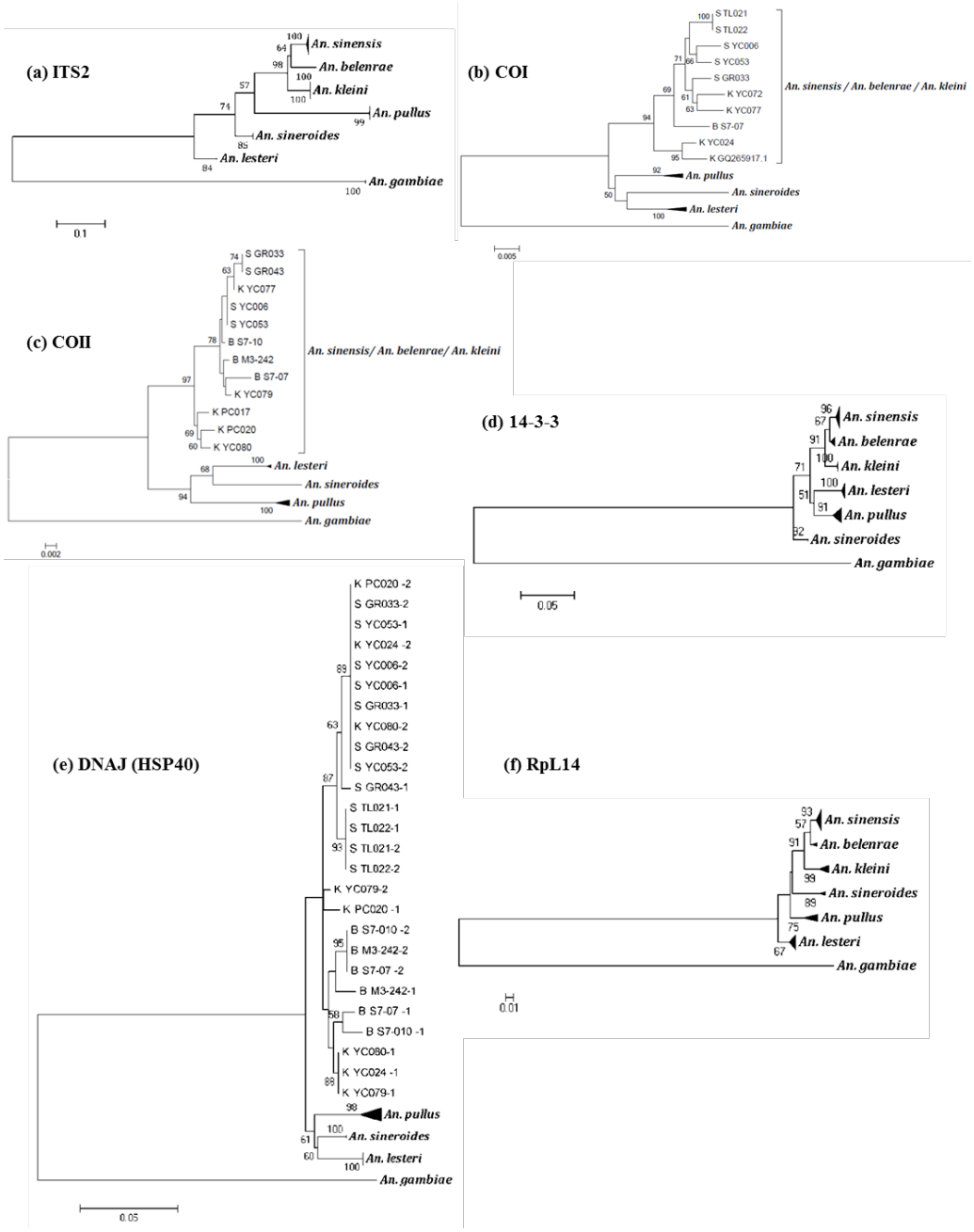

Figure 5. NJ phylogenetic trees as observed with different gene fragments in seven (six Korean and *An. gambiae*) *Anopheles* species. Numbers on the nodes represent the bootstrap values of 100 replications.

Species trees and divergence time estimation

Species trees based on all six genes supported the COI and COI + COII gene trees with high posterior probabilities and likelihood values (Figure 6). Since the COI and COI+COII gene trees were congruent and both genes were evolving under the molecular clock hypothesis, both sequences from a total of seven *Anopheles* species (the six Korean species with one *An. gambiae*) were used to estimate divergence times. *A. aegypti* COI and COII sequences were used for calibration and out-groups. However, inference within the *An. sinensis* complex was bypassed because there was incomplete lineage sorting among the mitochondrial DNA sequences (Figure 5 b and c). The split of *An. sinensis* s.s. and *An. belenrae* was 7.378 Myr (95% CI, 2.607–13.415 Myr), *An. sinensis* s.s. and *An. kleini* 12.842 Myr (95% CI, 5.331–22.738 Myr), and *An. kleini* and *An. belenrae* 12.832 Myr (95% CI, 5.366–22.738 Myr) (Figure 7). The divergence time of *An. lesteri* and *An. sineroides* was 19.936 Myr (95 % CI, 8.720–32.858 Myr), that of *An. lesteri* and *An. pullus* was 24.756 Myr (95% CI, 11.809–38.939 Myr), and that of *An. pullus* and *An. sineroides* was 24.215 Myr (95% CI, 10.993–38.547 Myr).

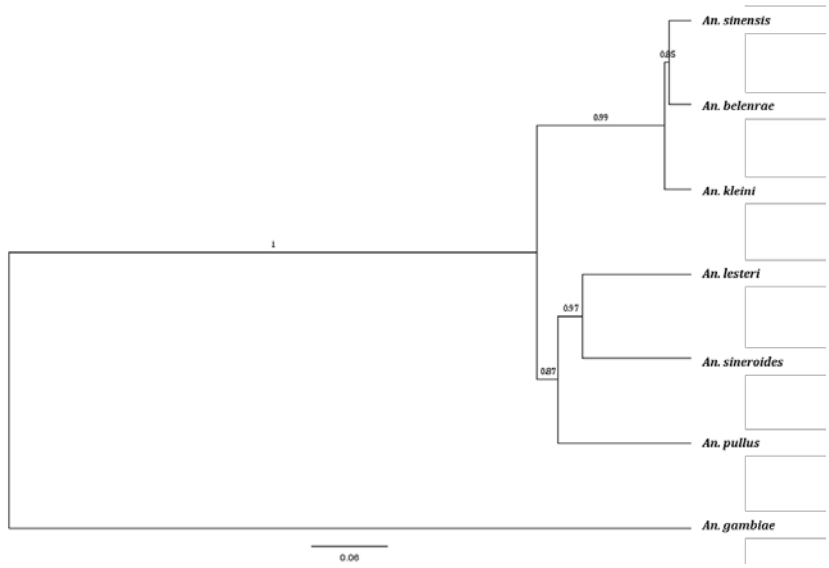

Figure 6. Estimate of the species tree based on a combined dataset constructed using *BEAST.

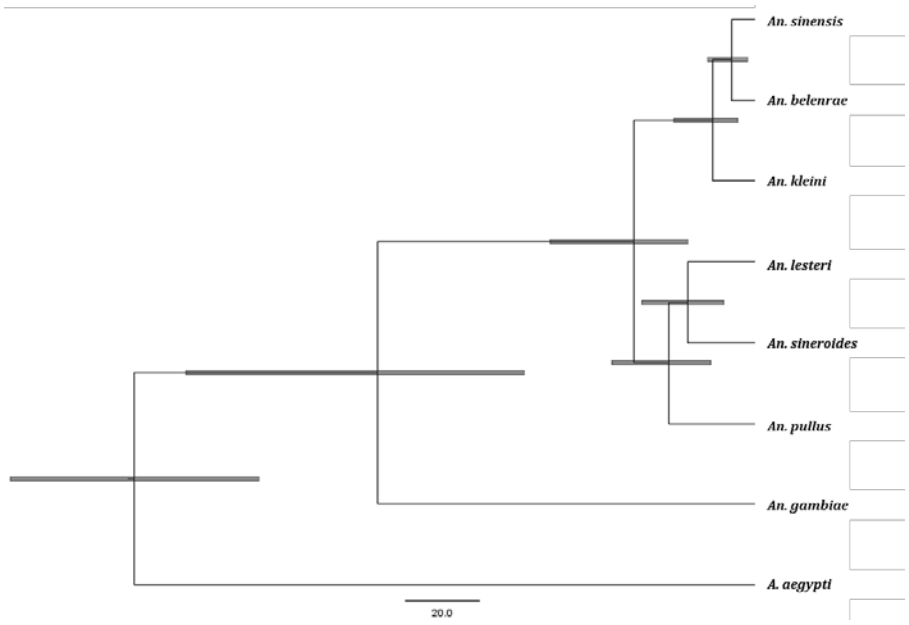

Figure 7. Phylogenetic tree constructed using BEAST based on COI and COII datasets with the substitution rate defined as 2.3%/Myr. The gray bars indicate the 95% highest posterior density (HPD) intervals.

Polymorphism, recombination, and divergence analyses

The absence of recombination was one of the assumptions of the IM model used in this study. Therefore, all sequences were checked for recombination and a non-recombining (NR) block was finally chosen for subsequent analyses (Table 3). Another assumption of the IM model was that the variation within the data set was neutral. In order to fulfill this requirement, Tajima's *D* tests of neutrality were used. No significant deviations were observed after Bonferroni correction.

The minimum number of recombination events for each gene and summaries of polymorphism information for both the whole blocks and the NR blocks are shown in Table 3. Of the six loci, the two loci, 14-3-3ζ and RpL14, included both coding and non-coding regions, three loci, COI, COII, and DNAJ (HSP40), included only coding regions, and ITS2 included only non-coding regions. Overall genetic diversity values of *An. kleini* were higher than those of *An. sinensis* s.s., except for in the 14-3-3ζ gene. As seen in Table 4, genetic differentiation between the two species based on F_{ST} estimates was high, ranging from 0.27 to 1.0, using both whole fragments and NR blocks.

Table 3. Polymorphisms between *An. sinensis* s.s. and *An. kleini*.

Locus	Species	RM	Length(bp)	N	S	π	θ	Tajima's D
COI	*An. sinensis*	6	658	11	16	0.00613	0.00830	-1.1638
			(345)	(10)	(7)	(0.00651)	(0.00717)	(-0.3936)
	An. kleini			9	25	0.01659	0.01476	0.6139
				(7)	(14)	(0.01794)	(0.01656)	(0.4587)
COII	*An. sinensis*	0	726	15	10	0.00184	0.00424	-2.1560
	An. kleini			14	18	0.00739	0.00866	-0.61576
ITS2	*An. sinensis*	0	536	32	0	0	0	0
	An. kleini		517	28	0	0	0	0
RpL14	*An. sinensis*	5	428	20	34	0.01866	0.02408	-0.8890
			(259)	(15)	(12)	(0.01399)	(0.01496)	(-83954)
	An. kleini			18	28	0.02536	0.03255	-0.88636
				(17)	(20)	(0.02220)	(0.02844)	(-0.86848)
DNAJ (HSP40)	*An. sinensis*	2	433	26	3	0.00053	0.00182	-1.7336
			(415)	(26)	(3)	(0.00053)	(0.00182)	(-1.7336)
	An. kleini			26	17	0.01211	0.01089	0.39545
				(20)	(10)	(0.00938)	(0.00681)	(1.3219)
14-3-3ζ	*An. sinensis*	13	497	28	6	0.00420	0.00497	-0.4732
			(496)	(25)	(5)	(0.00270)	(0.00325)	(-0.4850)
	An. kleini			22	1	0.00063	0.00056	0.23682
				(22)	(1)	(0.00063)	(0.00056)	(0.23682)
GCSβ	*An. sinensis*	0	143	28	4	0.00525	0.00719	-0.70398
	An. kleini			26	0	0	0	0

Numbers in parentheses are related to the NR block for each locus.

RM, minimum number of recombination events; N, number of sequences for each species for each locus; S, Number of segregating sites; π, the average number of nucleotide differences per site between two sequences; θ, Theta(π)=4Nμ from number of segregating sites.

Table 4. Genetic differentiation between *An. sinensis* s.s. and *An. kleini*.

Locus	F_{ST}	N_m	D_{XY}	D_a	Fixed	Shared
COI	0.33086^{ns}	0.51	0.01723	0.00570	0	6
	0.35116^{ns}	0.46	0.01884	0.00662	0	1
COII	0.27142^{ns}	0.67	0.00633	0.00172	0	4
ITS2	1.00000*	0.00	0.07946	0.07946	41	0
RpL14	0.67259*	0.12	0.06606	0.04443	0	6
	0.74414**	0.09	0.06457	0.04805	0	2
DNAJ (HSP40)	0.60237**	0.17	0.01590	0.00958	0	2
	0.58138***	0.18	0.01165	0.00677	0	1
14-3-3ζ	0.88755***	0.03	0.01955	0.01735	6	0
	0.91018***	0.02	0.01926	0.01753	6	0
GCSβ	0.94688***	0.01	0.05051	0.04783	4	0

F_{ST}, pairwise fixation index; *** significant at $P < 0.0001$; ** significant at $P < 0.001$; * significant at $P < 0.01$; ^{ns}, non-significant, $P > 0.01$; *N*m, estimated number of migrants per generation between populations calculated from F_{ST}; *D*xy, average number of nucleotide substitutions per site between populations; *D*a, number of net nucleotide substitutions per site between populations; Fixed, number of fixed differences between species; Shared, number of shared polymorphic sites between species.

Selection tests

Sequences from all populations were used to estimate selection, but only the four nuclear loci with sequences from coding regions (DNAJ (HSP40), RpL14, 14-3-3ζ, and GCSβ) were carried out for the test. The d_N/d_S ratios for the four loci were: DNAJ (HSP40)=0.0489, RpL14=0.969, 14-3-3ζ=1.227, and GCSβ=50. Of the four loci, RpL14, 14-3-3ζ, and GCSβ had overall d_N/d_S ratios higher than 0.5 and are thus candidates to be under selection (Swanson and Vacquier 2002; Almeida and DeSalle 2008).

Genealogy analysis

Gene genealogy analyses for both whole sequences and NR blocks were conducted using NJ (Figure 8). The gene trees of three loci (ITS2, 14-3-3ζ, and GCSβ) clearly grouped the sequences from *An. sinensis* s.s. and *An. kleini* in different clusters.

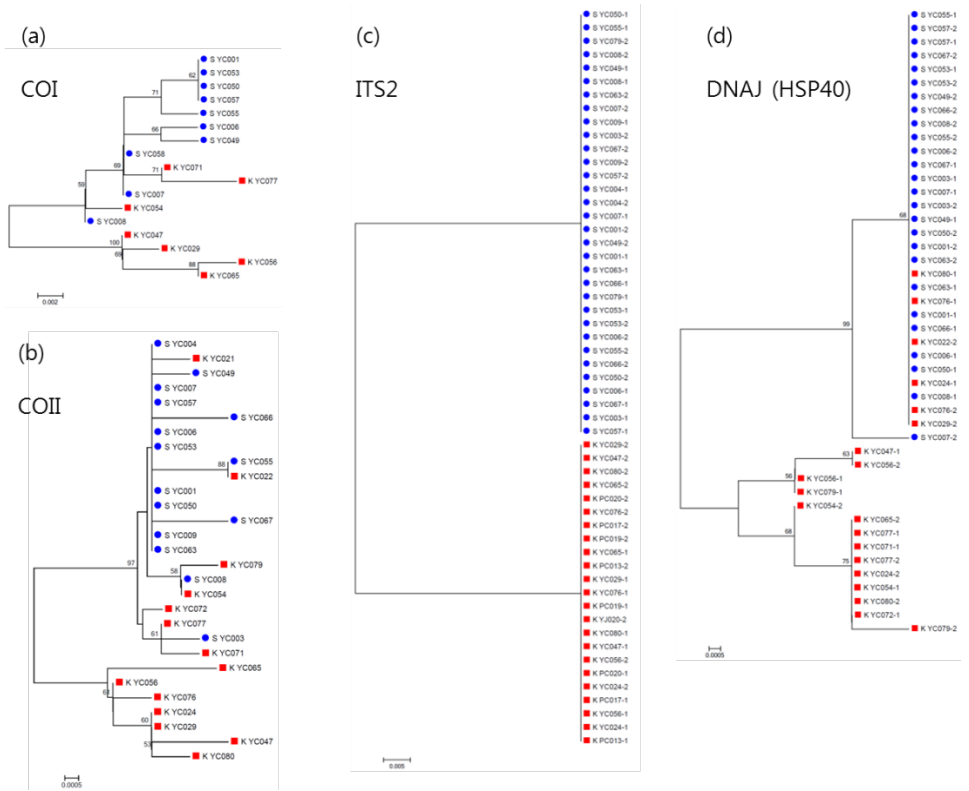

Figure 8. NJ phylogenetic trees as observed with different gene fragments in *An. sinensis* s.s. and *An. kleini*. Blue circles and red squares indicate individual sequences of *An. sinensis* s.s. and *An. kleini*, respectively. Numbers on the nodes represent the bootstrap values of 100 replications.

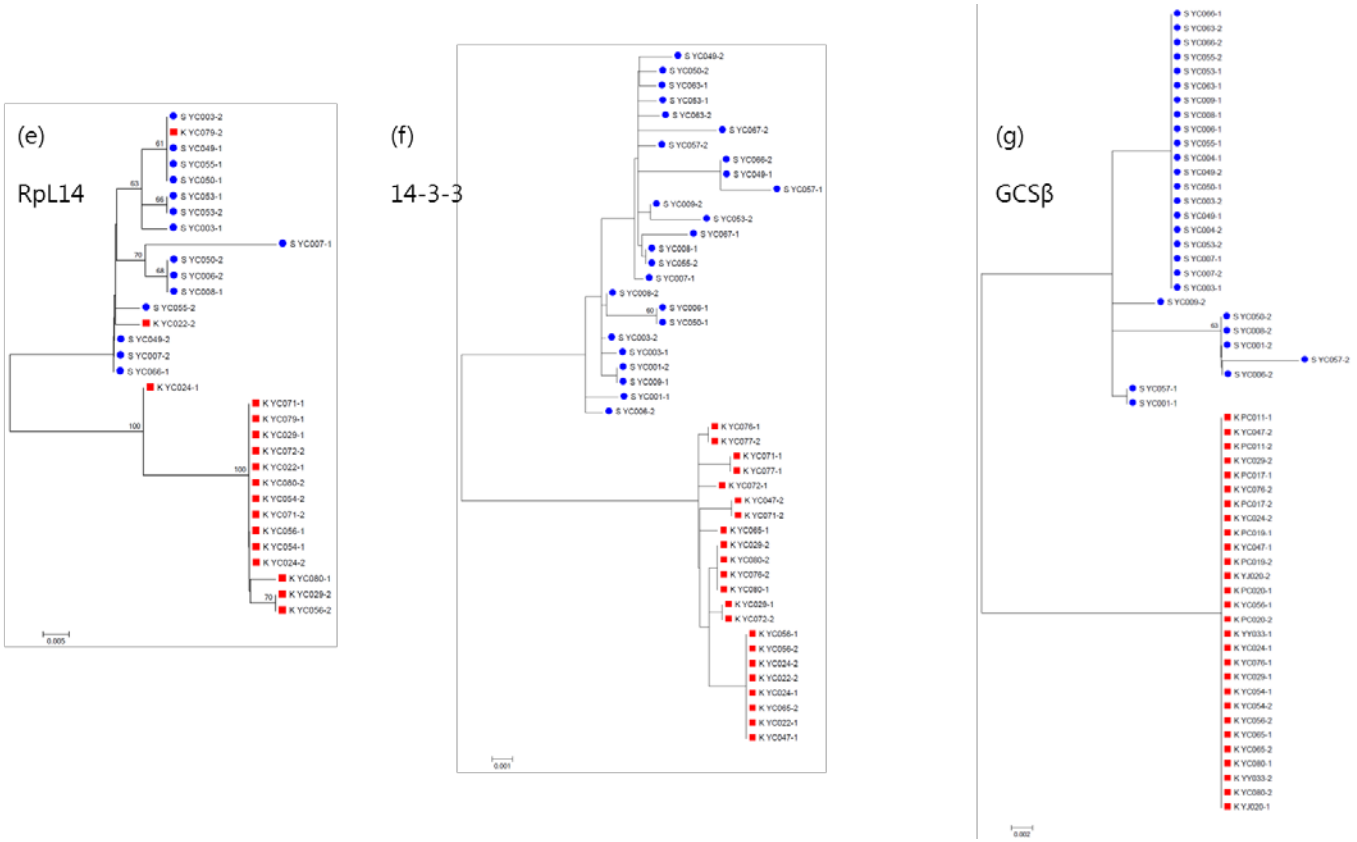

Figure 8. Continued.

Isolation and introgression

A population divergence analysis under the IM model using multiple loci was performed using the IM program to estimate directional migration rates (m_1 and m_2) between *An. sinensis* s.s. and *An. kleini*. Following the IM model assumptions, only the NR blocks were used and some putatively recombinant sequences were excluded before the IM analysis (Table 3). The directional migration rates were varied across loci (Figure 9; Table 5). The loci that are under selection, RpL14, 14-3-3ζ, and GCSβ, had near-zero migration in either direction. Clear evidence of asymmetric introgression of *An. kleini* DNAJ (HSP40) into *An. sinensis* s.s. was observed.

Table 5. Migration rate and maximum-likelihood estimates for *An. sinensis* s.s. and *An. kleini*.

	m_1		m_2	
	HiPt	90HPD	HiPt	90HPD
COI	0.005	0.0050- 8.2850	0.215	0.0050-8.0750
COII	0.005	0.0050-8.8150	0.765	0.0050-9.9950
ITS2	0.005	0.0050-0.3150	0.005	0.0050-0.3150
DNAJ (HSP40)	0.005	0.0050-9.9950	2.595	0.0050-6.8650
RpL14	0.005	0.0050-1.8550	0.375	0.0050-4.9350
14-3-3ζ	0.005	0.0050-0.6550	0.005	0.0050-2.2650
GCSβ	0.005	0.0050-0.8050	0.005	0.0050-3.1050
Selected loci	0.005	0.0050-0.1550	0.285	0.0650-0.7950

m, migration rate (m_1, from *An. sinensis* s.s. to *An. kleini*; m_2, from *An. kleini* to *An. sinensis* s.s.); HiPt, value of the bin with the highest count; HPD90, lower (HPD90Lo) and upper (HPD90Hi) bounds of the estimated 90% highest posterior density (HPD) interval.

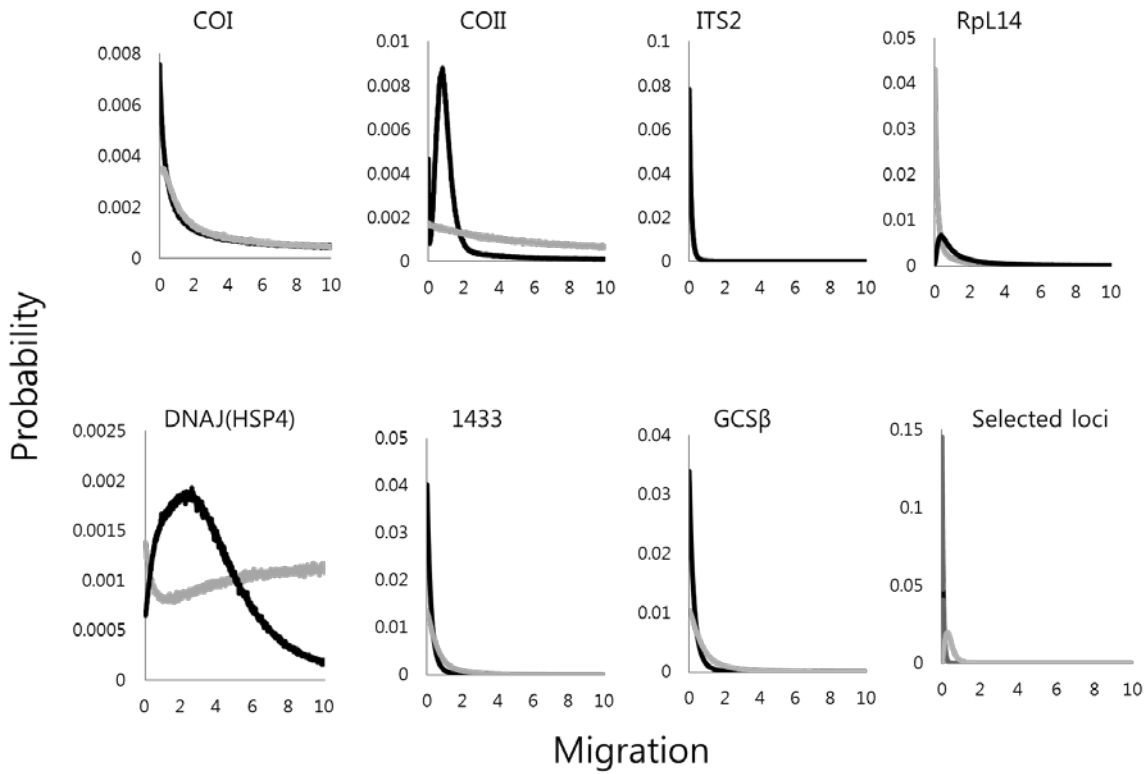

Figure 9. Posterior probability estimates of migration parameters (scaled by mutation rate) between *An. sinensis* s.s. and *An. kleini*. Black lines show m_1 (migration forward in time from *An. sinensis* s.s. to *An. kleini*) and gray lines show reverse migration (m_2) for each of the loci analyzed (in ITS2 the lines are superimposed). Numbers above lines indicate the maximum likelihood values. Numbers below each graph show the 90% highest posterior density (HPD) intervals of migration rates m_1 and m_2.

Discussion

The biological species concept defines species as groups of naturally interbreeding populations that are reproductively isolated from other species (Mayr 1963). Hybridization and gene introgression are not easily disturbing to individuals within a species sharing defining properties (Coyne and Orr 2004). However, recently diverged species will share alleles throughout their genomes as mosaic patterns caused by non-random sorting of ancestral polymorphism and differential introgression among genetic regions (Ting et al. 2000). Usually, there are relatively few loci that will experience frequent strong natural selection and are not free to move across species boundaries, and these loci will become entirely or almost fixed in each species. Thus, genes will show different patterns of variation depending on natural selection effects, recombination rates, linkage relationships, and contributions to reproductive barriers among closely related species.

Phylogenetic inference among six Hyrcanus group species indicates that three loci (ITS2, RpL14, and 14-3-3ζ) show complete lineage sorting and provide useful species identification tools, although they may not represent true phylogenetic relationships. Interestingly, the clade (*An. sinensis* s.s. + *An. belenrae*) + *An. kleini* is well supported not only by gene trees with different phylogenetic methods but also by species trees, which suggests that *An. sinensis* s.s. and *An. belenrae* are more closely related to each other than either is to *An. kleini,* even though incomplete lineage sorting was observed among the three species in COI, COII, and DNAJ (HSP4) gene trees. However, dis-concordant phylogenies with two

mitochondrial DNA fragments, COI and COII, were observed among *An. lesteri, An. pullus,* and *An. sineroides.* Incongruence between gene trees may result from the fact that the mode of evolution of the gene is generally influenced by the differential functions and levels of evolutionary forces (True and Carroll 2002), which might lead to different phylogenetic relationships among these three species.

Since the COI and COII gene trees were congruent with phylogenetic trees constructed by four different tree construction methods as well as with species trees based on all six genes, these two genes were enlisted to estimate species divergence times. It has been argued that in temperate regions the glacial periods triggering repeated isolation between refugees (Hugall et al. 2002; Moritz et al. 2009) were too short for reproductive isolation and that the majority of speciation events probably predate the Pleistocene (Zink and Slowinski 1995; Knowles 2000). The present estimates of the split times of the six Korean *Anopheles* Hyrcanus group were 7.3–34 Myr, supporting the previous hypothesis. Furthermore, it has been proposed that two subgenera, *Anopheles* and *Ceillia*, diverged at 90–100 Myr (Krzywinski et al. 2006). The present estimate of the divergence time between *An. sinensis* s.s. and *An. gambiae*, 103 Myr (95% CI, 62.079–150.1673 Myr), therefore, is consistent with previous studies.

Apparently different estimates of selection pressure among loci were observed in *An. sinensis* s.s. and *An. kleini.* Alleles at strongly selected loci may have near-zero introgression rate estimates, because these alleles are not free to move across species boundaries. Among four nuclear coding loci, the cell survival,

apoptosis, and signal transduction related gene 14-3-3ζ, the ribosomal protein gene RpL14, and the soluble guanylyl cyclase beta subunit gene GCSβ, had d_N/d_S values greater than 0.9 and near-zero introgression estimates with 90% highest posterior densities.

Directional migration rates among seven loci between *An. sinensis* s.s. and *An. kleini* were varied both in magnitude and direction (Figure 9; Table 5). Although the analyses here have violated one of the IM assumptions (neutrality), the effects these violations are not yet fully understood (Maroja et al. 2009). The two directional introgression rates for DNAJ (HSP40), the neutral loci, showed that m_2 (the introgression rate from *An. kleini* to *An. sinensis* s.s.) was greater than m_1 (the introgression rate from *An. sinensis* s.s. to *An. kleini*), whereas the joint posterior probability estimates of directional migration rates for the three loci that are under selection pressure combined were near-zero in both directions. Thus, *An. kleini* alleles are unidirectionally flowing into *An. sinensis* s.s., but gene flow from the opposite direction is low or absent. This one-way incompatibility is consistent with a previous hybrid study demonstrating that all F_1 hybrids carry *An. kleini* mitochondrial DNA and hybrid females back-crossed with a normal *An. sinensis* s.s. specimens show normal fertility (Joshi et al. 2009). This post-mating barrier would obviously limit introgression from *An. sinensis* s.s. into *An. kleini* genome-wide.

Asymmetric introgression maybe relatively common and has been documented in a variety of insects, such as the *An. gambiae* complex (Besansky et

al. 2003), *Heliconius* butterflies (Kronforst et al. 2006), and *Gryllus* crickets (Maroja et al. 2009). The moderate levels of genetic diversity and lack of significant Tajima's *D* among *An. sinensis* s.s. and *An. kleini* suggest speciation without population bottlenecks. Observed shared polymorphisms between species at most loci suggest that current observed patterns of variation may result from a combination of gene flow and unsorted ancestral polymorphism (Maroja et al. 2009). As taxa are expected to become reciprocally monophyletic only after many ($> 9N_e$) generations, ancestral polymorphism would persist even after species barriers were completed with no hybridization (Tajima 1983; Neigel and Avise 1986; Harrison 1991; Hey 1994; Maddison 1997; Hudson and Coyne 2002). In this scenario, *An. sinensis* s.s. and *An. kleini* are still exchanging genes and it will take a long time to reciprocally complete monophyly. Even if a locus showing introgression in this study is not directly related to epidemiologically important gene functions, the results obtained here remain especially important in showing that the both species have different vector competence (Joshi et al. 2011). Further in-depth analyses on many genome-wide datasets are needed to prove the current epidemiological and evolutionary dynamics between *An. sinensis* s.s. and *An. kleini*.

CHAPTER 2. The Polymorphism and the Geographical Distribution of the Knockdown Resistance (*kdr*) of *Anopheles sinensis* in the Republic of Korea

Introduction

The use of insecticides has been the most effective and economical vector control method for malaria and other vector-borne diseases, such as dengue and filariasis (Rivero et al. 2010). Since the first introduction of pyrethroids and organophosphates to the ROK in the 1970s, these insecticides have been used throughout the country in order to control medically and agriculturally important arthropod pests, including mosquitoes. The national malaria eradication programme that was based mostly on the chemical control of vector mosquitoes was successful in the 1990s in the ROK. However, overdoses of insecticide have quickly led to the presence and spread of insecticide-resistant mosquitoes (Ree 2005), which have caused serious problems for malaria-controlling interventions.

Resistance to pyrethroids and DDT, which is known as knockdown resistance (*kdr*), is caused by a single mutation in the S6 transmembrane segment of domain II in the voltage-gated sodium channel (VGSC) gene (Hemingway et al. 2004). Several mutations at codon 1014, such as L1014F (Leu-to-Phe), L1014S

(Leu-to-Ser), and L1014C (Leu-to-Cys) have been reported in many *Anopheles* species, including *Anopheles gambiae*, *Anopheles arabiensis*, *Anopheles culicifacies*, *Anopheles stephensi*, *An. sinensis* complex, *Anopheles sacharovi*, *Anopheles subpictus*, *Anopheles sundaicus*, *Anopheles aconitus*, and *Anopheles vagus* (Martinez Torres et al. 1998; Luleyap et al. 2002; Enayati et al. 2003; Diabate et al. 2004; Hoti et al. 2006; Karunaratne et al. 2007; Kim et al. 2007; Syafruddin et al. 2010). A positive correlation between the *kdr* genotype and the resistance phenotype to pyrethroids and DDT in the *Anopheles* species was well documented by articles (Kim et al. 2007; Donnelly et al. 2009; Tan et al. 2012).

A previous study reported that the frequencies of the *kdr* allele of *An. sinensis* in the ROK ranged from 25.0 to 96.6%, which suggested that pyrethroid resistance was already widespread in natural populations of the ROK (Kim et al. 2007). A standard WHO insecticide susceptibility test was conducted on the *Anopheles* species in the ROK (Ree and Paik 1967; Shin et al. 2003; Chang et al. 2009), and the results showed the development and widespread distribution of pyrethroid-resistant phenotypes. In order to monitor knockdown mutations of pyrethroid resistance in *An. sinensis*, real-time PCR amplification of a specific allele (rtPASA) has been developed. The results suggested that L1014F mutation was a major allele that showed a high allele frequency, whereas L1014C mutation was a minor allele that showed a low allele frequency within the *An. sinensis* populations in the ROK (Kim et al. 2007). However, these previous studies conducted chemical and molecular assays on the *An. sinensis* group and species-specific assays have

never been conducted because the sibling species are morphologically indistinguishable, and, unlike *An. sinensis* s.s., the other species have relatively low population densities. Because the mechanisms and degree of insecticide resistance vary among species and populations (Awolola et al. 2003; Cui et al. 2006; Chen et al. 2010; Verhaeghen et al. 2010), the present study aimed to explore the species-specific distribution of *kdr* resistance alleles in all members of the Hyrcanus group mosquitoes in the ROK.

Materials and Methods

Mosquito collections and species identification

Mosquitoes were collected from 22 locations (Figure 10; Table 6) in the ROK with a CDC Miniature Light Trap (John W Hock Company, Gainesville, FL, USA) and preserved on site using dry ice. Because it is morphologically hard to distinguish the species within the *An. sinensis* complex, the mosquito specimens were isolated based on their morphological characteristics that were determined first under a stereomicroscope in the laboratory compared to the other insects, and then the specific species of all of the *Anopheles* specimens were identified using multiplex assays (Joshi et al. 2010). DNA was extracted from the entire body or legs by following a standard phenol extraction protocol or DNeasy Blood and Tissue kit (QIAGEN, USA).

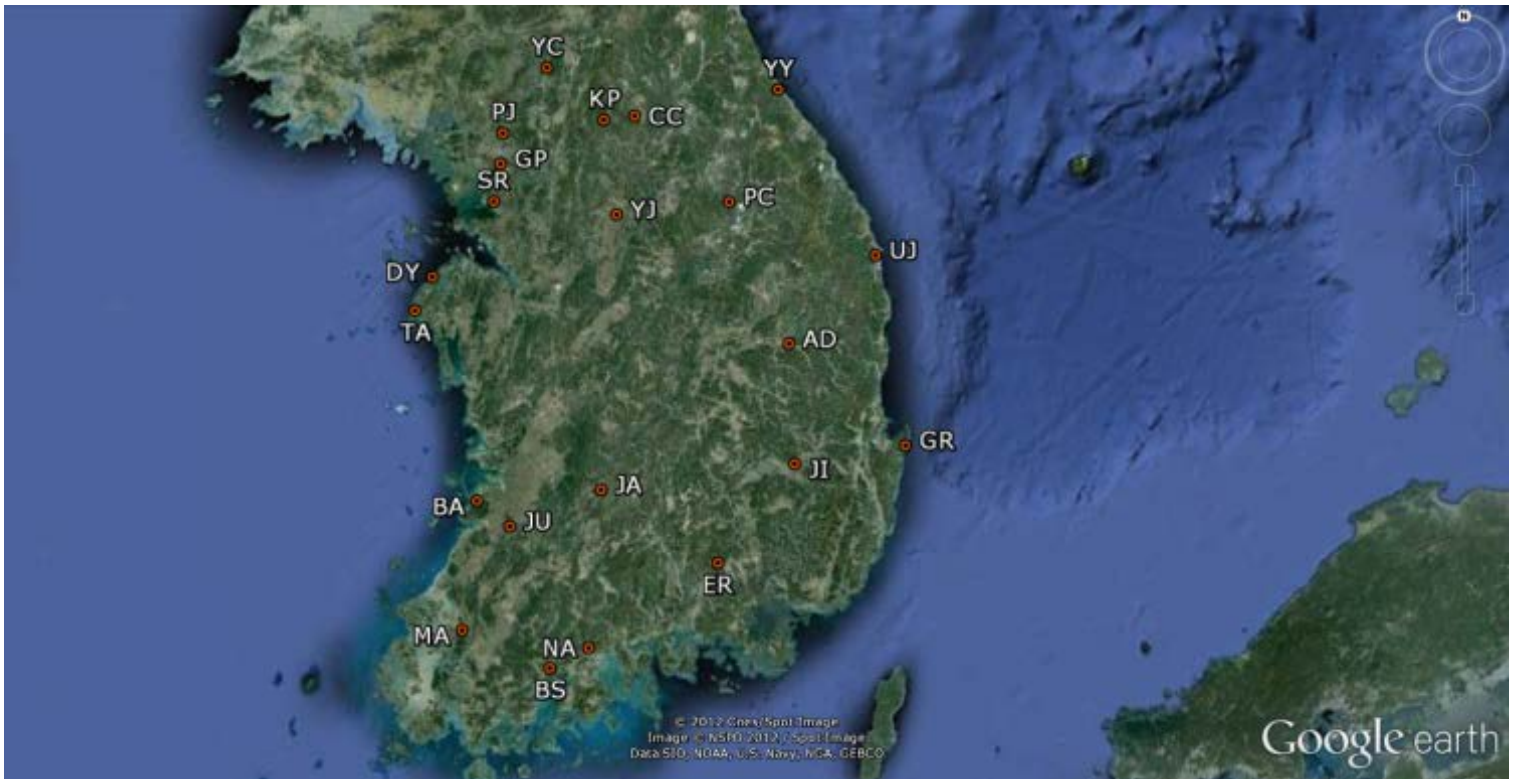

Figure 10. A map of the ROK showing the geographical locations of the sampling sites.

Table 6. Summary of regional information and species composition.

Name	Sample sites	N	Identified Species					
			An. sinensis	*An. pullus*	*An. kleini*	*An. belenrae*	*An. lesteri*	*An. sineroeides*
AD	ANDONG	16	16	0	0	0	0	0
BA	BUAN	16	16	0	0	0	0	0
BS	BOSEONG	13	13	0	0	0	0	0
CC	CHOONCHEON	8	8	0	0	0	0	0
DY	DANYANG	15	15	0	0	0	0	0
ER	EUIRYEONG	25	25	0	0	0	0	0
GP	GIMPO	237	208	10	5	2	12	0
GR	GURYONGPO	17	17	0	0	0	0	0
JA	JINAN	11	11	0	0	0	0	0
JI	JAIN	29	29	0	0	0	0	0
JU	JEONGEUP	10	10	0	0	0	0	0
KP	KAPYEONG	14	14	0	0	0	0	0
MA	MOOAN	6	6	0	0	0	0	0
NA	NAKAN	28	28	0	0	0	0	0
PC	PYEONGCHANG	8	0	0	8	0	0	0
PJ	PAJOO	127	114	13	0	0	0	0
SR	SORAE	25	24	0	0	0	1	0
TA	TAEAN	12	12	0	0	0	0	0
UJ	ULJIN	16	16	0	0	0	0	0
YC	YEONCHEON	80	62	3	15	0	0	0
YJ	YEOJOO	12	11	0	1	0	0	0
YY	YANGYANG	30	10	0	1	0	0	19
		755	665	26	30	2	13	19

DNA sequencing of VGSC

In order to detect the *kdr* mutation, part of the IIS6 domain of the VGSC was PCR amplified and directly sequenced using 5′ASIIS56 and 3′ASIIS56 intron primers (Kim et al. 2007). The sequences were determined using an ABI 3730xl DNA analyser (Applied Biosystems, USA) and visually confirmed using Sequence Navigator 1.1 software (Applied Biosystems, USA). The obtained sequences were aligned with Clustal X version 2.0 (Larkin et al. 2007). The deduced amino acid comparisons were conducted by MEGA 5.05 (Tamura et al. 2011).

Statistical analyses

The maximum likely frequency (y) of an allele present or absent in a sample of a given size (x) was obtained from the upper of 95% confidence limit of binomial distribution, given by $y=1-0.05^{1/x}$, following the example of Post and Millest (Post and Millest 1991).

Results

Species composition and distribution

A total of 755 *Anopheles* Hyrcanus group mosquitoes were collected from 22 sites in the ROK, as briefly described in Figure 10 and Table 6. As a result of the molecular identifications that were conducted by multiplex assays (Table 6), most of the specimens were *An. sinensis* s.s. (665 of 755, 88.08%), which is known as the dominant species in the ROK, and these were followed by *An. kleini* (30 of 755, 3.97%), *An. pullus* (26 of 755, 3.44%), *An. sineroides* (19 of 755, 2.52%), *An. lesteri* (13 of 755, 1.72%), and *An. belenrae* (two of 755, 0.26%). Hybrid

individuals were not detected. *An. sinensis* s.s. was found at most of the sites (21 of 22), whereas the other species were found at a few sites (one to five of 22) in the northern part of the ROK, and these results were in concordance with previous studies showing topoclinal distributions.

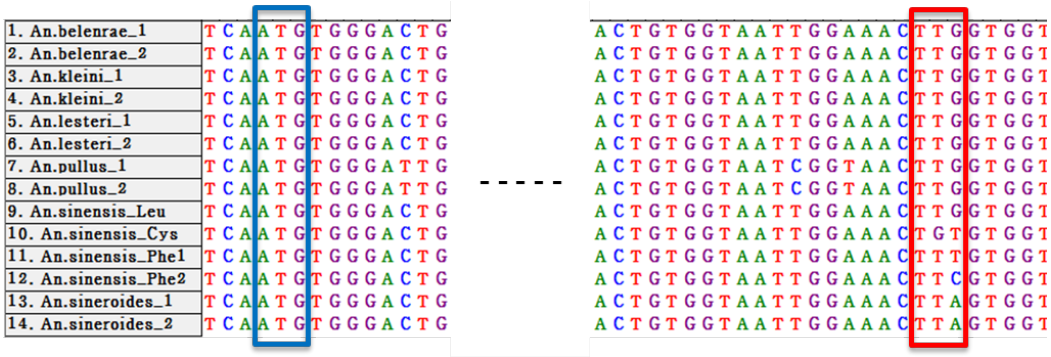

Figure 11. Alignment of multiple DNA sequences at codon 918 and codon 1014 within the VGSC gene in six Hyrcanus group mosquitoes in the ROK. The blue box indicates codon 918 and the red box indicates codon 1014.

kdr mutations

In order to examine the mutations at codon 1014, 343-bp sequences of part of the IIS6 domain of the VGSC gene were obtained from a total of 177 specimens that consisted of *An. sinensis* s.s. (n = 87), *An. kleini* (n = 30), *An. pullus* (n = 26), *An. belenrae* (n = 2), *An. lesteri* (n = 13), and *An. sineroides* (n = 19) from 10 sites in the ROK (Table 7 and 8). The DNA sequences were different among the species. However, the deduced amino acid sequences showed no non-synonymous mutations within the VGSC-coding regions in all six species, except for at codon 1014. Pyrethroid- and DDT-resistant *kdr* mutations were detected in *An. sinensis* s.s.

only, and the other five species had the wild-type *kdr* allele L1014 only (Figure 11; Table 7 and 8). Interestingly, *An. sineroides* had a different amino-acid coding sequence (TTA). But the same amino acid (leucine) occurred at codon 1014. Met-Thr mutation at codon 918 (M918T), or super-*kdr*, which enhances the resistance in combination with L1014F within the same genetic region was not detected in any of the six species.

Table 7. Species-specific genotype frequencies of the *kdr* allele at each study site.

Study Sites	Species	N	Genotype Frequency (%)									
			L/L	L*/L*	L/P	L/C	P/P	P/C	C/C	L/P*	P/P*	C/P*
YC	*An. sinensis*	14	14.3	0	14.3	7.1	28.6	35.7	0	0	0	0
	An. kleini	15	100	0	0	0	0	0	0	0	0	0
	An. pullus	3	100	0	0	0	0	0	0	0	0	0
PJ	*An. sinensis*	17	11.8	0	17.6	0	41.2	23.5	5.9	0	0	0
	An. pullus	13	100	0	0	0	0	0	0	0	0	0
GP	*An. kleini*	5	100	0	0	0	0	0	0	0	0	0
	An. lesteri	12	100	0	0	0	0	0	0	0	0	0
	An. belenrae	2	100	0	0	0	0	0	0	0	0	0
	An. pullus	10	100	0	0	0	0	0	0	0	0	0
PC	*An. kleini*	8	100	0	0	0	0	0	0	0	0	0
YJ	*An. kleini*	1	100	0	0	0	0	0	0	0	0	0
BS	*An. sinensis*	13	0	0	15.4	0	46.2	30.8	7.7	0	0	0
SR	*An. lesteri*	1	100	0	0	0	0	0	0	0	0	0
AD	*An. sinensis*	16	50	0	0	31.3	0	0	0	18.8	0	0
GR	*An. sinensis*	17	58.9	0	11.8	0	0	0	0	0	23.5	5.9
YY	*An. sinensis*	10	0	0	30	0	60	0	0	10	0	0
	An. kleini	1	100	0	0	0	0	0	0	0	0	0
	An. sineroides	19	0	100	0	0	0	0	0	0	0	0
		177										

L indicates the susceptible allele L1014 (TTG), and L* indicates the other susceptible allele, L1014 (TTA). P indicates the resistance allele L1014F (TTT), and P* indicates the other codon type of allele L1014F (TTC). C indicates the resistance allele L1014C (TGT).

Table 8. Species-specific allele frequencies of the *kdr* allele (with 95% confidence intervals, CI) for each study site.

Study Sites	Species	N	*kdr* Allele Frequency (%)			
			Susceptible	Resistant		
			Leu	Phe		Cys
			TTG[95% CI]	TTT[95% CI]	TTC[95% CI]	TGT[95% CI]
YC	*An. sinensis*	14	25.0[20.2-29.8]	54.0[43.6-64.4]	0.0[0.0-0.0]	21.0[17.0-25.0]
	An. kleini	15	100.0[81.9-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
	An. pullus	3	100.0[36.8-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
PJ	*An. sinensis*	17	20.6[17.3-23.9]	61.8[51.8-71.7]	0.0[0.0-0.0]	17.6[14.8-20.5]
	An. pullus	13	100.0[79.4-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
GP	*An. kleini*	5	100.0[54.9-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
	An. lesteri	12	100.0[77.9-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
	An. belenrae	2	100.0[22.4-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
	An. pullus	10	100.0[74.1-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
PC	*An. kleini*	8	100.0[68.8-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
YJ	*An. kleini*	1	100.0[5.0-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
BS	*An. sinensis*	13	7.7[6.1-9.3]	69.2[55.0-83.5]	0.0[0.0-0.0]	23.1[18.3-27.8]
SR	*An. lesteri*	1	100.0[5.0-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
AD	*An. sinensis*	16	75.0[62.2-87.8]	0.0[0.0-0.0]	9.0[7.5-10.5]	16.0[13.3-18.7]
GR	*An. sinensis*	17	64.7[54.3-75.2]	17.6[14.8-20.5]	14.7[12.3-17.1]	2.9[2.5-3.4]
YY	*An. sinensis*	10	23.5[17.4-29.6]	70.6[52.3-88.9]	5.9[4.4-7.4]	0.0[0.0-0.0]
	An. kleini	1	100.0[5.0-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
	An. sineroides	19	100.0*[85.4-100.0]	0.0[0.0-0.0]	0.0[0.0-0.0]	0.0[0.0-0.0]
		177				

The asterisk indicates TTA L1014 allele frequency.

Anopheles sinensis s.s.

A total of four types, which consisted of one wild type (TTG L1014) and three mutant types (TTT L1014F, TTC L1014F, and TGT L1014C), of *kdr* alleles were detected in *An. sinensis* s.s.. TTC L1014F was found for the first time. TTT L1014F was the dominant mutation in all of the regions, whereas TTC L1014F, which was distributed in the eastern part of the ROK alongside the Taebaek Mountain (YY, AD, and GR in Figure 10; Table 7 and 8), existed only in the heterozygotic state (Table 7). The allele frequencies of L1014 ranged from 7.7% to 75.0%, while that of L1014F (TTT) ranged from 0% to 70.6%, that of L1014F (TTC) ranged from 0% to 14.7%, and that of L1014C ranged from 0% to 23.1% (Table 8).

Discussion

Knockdown resistance (*kdr*) is caused by mutations at codon 1014 of the VGSC, which is the target of pyrethroids and DDT. In this study, molecular analysis of the VGSC in the Hyrcanus group mosquitoes in the ROK revealed that mutations at codon 1014 existed only in *An. sinensis* s.s., whereas no *kdr* mutations were observed in the other five species, including *An. pullus, An. kleini, An. sineroides, An. lesteri,* and *An. belenrae*. For wild-type L1014, a previous comparative study of the VGSC of various taxa showed different usages of coding triplets at L1014 (Davies et al. 2007), while in the present results, the amino-acid coding sequences at L1014 differed between the species. The codon of L1014 was TTC in five species (*An. sinensis* s.s., *An. pullus, An. kleini, An. lesteri,* and *An. belenrae*), whereas, for *An. sineroides,* it was TTA, which is observed in a number of species, including *An.*

gambiae, *An. arabiensis*, and *An. vagus* (Martinez Torres et al. 1998; Diabate et al. 2004; Syafruddin et al. 2010).

Pyrethroids have been widely used in large quantities for the control of agricultural pests and medically important arthropod pests through thermal fogging, residual spraying, impregnated clothing, and mosquito nets since their introduction to the ROK in the 1970s. Inevitably, a variety of mosquitoes, including malaria vectors, might have developed resistance to pyrethroids and jeopardized the successful malaria control programmes in the ROK (Shin et al. 2003; Kim et al. 2007; Chang et al. 2009). A number of recent studies have reviewed the numerous cases that were examined and whether there were correlations between mutations in the VGSC and the resistance phenotype in diverse taxa (Davies et al. 2007; Soderlund 2008; Donnelly et al. 2009). Almost all of the results of the previous studies have shown a strong causal relationship between the *kdr* genotype and insecticide susceptibility to pyrethroids and DDT. However, the absence of a *kdr* mutation is not a causal factor of total susceptibility to the insecticides.

Although the detailed research on fitness costs of *kdr* mutations, additional biochemical assays and specific gene expression studies are needed for future study, the highly polymorphic *kdr* gene that was observed only in *An. sinensis* s.s. and the absence of a *kdr* mutation in the other five species suggest two tentative hypotheses. First, because the anopheline species other than *An. sinensis* s.s. are geographically distributed in the northern part of the ROK near the DMZ, the absence of *kdr* mutations in these species may have resulted from migration of these *kdr*-free

mosquitoes from North Korea or the DMZ to the ROK to seek for blood sources, such as cows or pigs. Along the DMZ and in North Korea, the environment was unsuitable for the mosquitoes due to the lack of blood sources. However, the amount of insecticide used in North Korea and along the DMZ was much less than the amount used in the ROK, which reduces the insecticide selection pressure (Shim et al. 1997). This hypothesis is in concordance with the renowned hypothesis that the re-emergence of *P. vivax* in the ROK arose from North Korea through sporozoite-infected mosquitoes that dispersed from North Korea to the ROK across the DMZ (Chai 1997; Shim et al. 1997; Ree 1998; Chai 1999; Kho et al. 1999; Ree 2000). Second, the highly polymorphic *kdr* gene in *An. sinensis* s.s. (the dominant *Anopheles* mosquito in East Asia) in the ROK may be explained by their large population size and wide species range. The level of genetic variation within a species is generated by mutation and eliminated by genetic drift due to finite population size (Crow and Kimura 1970). Large population size and wide species range are precondition to polymorphism, as a large effective population size will have an increased genetic variability (Soulé 1976; Frankham 1996) and a higher rate of mutation (Fowlie and Krüger 2003).

For *An. sinensis* s.s., the geographical distribution of *kdr* alleles is supported by a previous study that examined the population genetic structure of *An. sinensis* using mitochondrial control regions, and the results suggested distinct subdivisions in the Northern Group (NG) and Southern Group (SG) in the ROK (Jung et al. 2007). The Great Mountains, such as the Sobaek and Taebaek

Mountains that cross the ROK from the northeast to southwest may play a major role as potent genetic barriers. These two groups have different genetic properties, such that the SG is genetically more diverse and has a larger number of private alleles and effective population size than the NG. A total of four *kdr* alleles including one wild type and three mutant types were observed in this study. The three types of alleles (TTG L1014, TTT L1014F, and TGT L1014C) were observed in both the NG and the SG. Whereas the TTC L1014F allele, which was the rarest allele and which was detected for the first time in *An. sinensis* s.s. in this study, was only detected in the SG (AD, GR, and YY in Figure 10 and Table 6 and 7).

In summary, the different allele statuses of *kdr* genes in the Hyrcanus group mosquitoes suggest the importance of monitoring insecticide susceptibilities and the resistance of target vectors in control programmes. Effective resistance monitoring that is based on species-specific insecticide bioassay tests, molecular studies of allele diversity, origins of insecticide resistance, and minor resistance mechanisms (behavioural and cuticular resistance) will be crucial for building successful malaria vector control programmes that can explain and predict the development and spread of insecticide resistance traits.

CHAPTER 3. Population Genetic Structure of the Malaria Vector *Anopheles sinensis* sensu stricto in East Asia

Introduction

Anopheline mosquitoes usually form large geographical demes, either because of recent expansion from relatively large and stable populations or extensive gene flow (Besansky et al. 1997; Donnelly and Townson 2000; Lehmann et al. 2003). However, physical barriers such as mountain ranges, oceans, rivers, and forests may impede gene flow between *Anopheles* species that lack or are short of migration abilities (Loaiza et al. 2011).

An. sinensis s.s. is abundant across East Asia from Korea, China, and Japan, to Indonesia, and it is the most dominant anopheline species in Korea. *An. sinensis* s.s. is known for variation in chromosomes (Baimai et al. 1993), mitochondrial DNA (Jung et al. 2007), and internal transcribed spacer 2 sequences (ITS2s) (Min et al. 2002). Two karyotypic forms, A (X, Y_1) and B (X, Y_2), have been described by cytogenetic studies in *An. sinensis* s.s. (Baimai et al. 1993). Both forms exist in Thailand, and only the B form occurs in China and Korea (Xu and Qu 1991; Min et al. 2002). In Korea and Japan, *An. sinensis* s.s. have been implicated as a primary malaria vector species, whereas it is poorly susceptible to *P. vivax* in Thailand (Somboon et al. 1994) and is only a secondary vector in China (Gao et al. 2004).

Despite the potential significance for malaria control, only a few population genetic studies on *An. sinensis* s.s. have been conducted. Jung et al. (Jung et al. 2007) hypothesized that the Taebaek and Sobaek Mountains in the ROK have promoted subdivision on *An. sinensis* s.s. into two groups based on mitochondrial control regions, while in China, two genetic pools with moderate genetic differentiation have been identified in the absence of any correlation with geographic distance or barriers (Ma et al. 2011).

It is important epidemiologically to understand genetic diversity, population structure, population dynamics, and geographical distribution of *An. sinensis* s.s. to provide insights for predicting the spread of important genes, such as insecticide- or malaria-resistance genes, or for identifying heterogeneities in disease transmission due to distinct vector populations (Lehmann et al. 2003).

In this study, the genetic structures of *An. sinensis* s.s. populations across East Asia were characterized using both mitochondrial and nuclear DNA markers. I conducted a genetic analysis of 23 populations from Korea, China, and Taiwan using mitochondrial sequence data and four microsatellite markers.

Materials and Methods

Sampling and DNA extraction

Mosquitoes were collected from Korea, China, and Taiwan with a CDC Miniature Light Trap (John W Hock Company, Gainesville, FL, USA) and preserved on site using dry ice. Because it is difficult to distinguish the species within the Hyrcanus group morphologically, the mosquito specimens were first separated based on their

morphological characteristics seen under the stereomicroscope in the laboratory, and then the final species determination of all of the *Anopheles* specimens was carried out by multiplex assays (Joshi et al. 2010). DNA was extracted from the entire body or the legs by standard phenol extraction or with a DNeasy Blood and Tissue kit from QIAGEN, USA.

Sequence analysis of mitochondrial control region

The sequences of mitochondrial regions from the ROK were those previously published by Jung et al. (Jung et al. 2007) (GenBank accession numbers: DQ466091–DQ466107). In order to amplify the 210-bp variable region of the mitochondrial control region, U415 (5′- CCTCCTAATAATTTTCCCC -3′) and L672 (5′- GGGTGATATTAATTATAGACC -3′) primers (Jung et al. 2007) were used. PCR mixtures were made up of 5× *Taq* polymerase buffer, an AT rich (80% AT content) 1-mM dNTP mix, each primer, 500 mM, 2.5–250 pg total DNA, and 0.04 U/μL of go*Taq* polymerase (Promega, Madison, WI, USA). The PCR conditions were as follows: initial denaturation at 94°C for 3 min, 30 cycles of denaturation at 94°C for 30 s, annealing at 45°C for 50 s, elongation at 72°C for 50 s, and final extension at 72°C for 7 min. The PCR products were sequenced with amplifying primers and a Big Dye terminator sequencing kit (Applied Biosystems) according to the manufacturer's instructions. After purification, the reaction products were analyzed on an ABI PRISM Genetic Analyzer 3100 (Applied Biosystems). Bidirectional sequences were aligned and visually examined by using Sequence Navigator v1.0.1 (Perkin Elmer-Applied Biosystems). The sequences

were aligned with Clustal X version 2.0 (Larkin et al. 2007) and were exported to the NEXUS and PHYLIP formats for data analyses.

Data analyses of mitochondrial control region

The frequency of each haplotype, number of haplotypes, gene diversity, nucleotide diversity, and theta (θ) values based on the number of polymorphic sites (S) and the mean value of pairwise differences (π) were calculated using DnaSP v5 (Librado and Rozas 2009). The distance matrices of pairwise F_{ST} and γ_{ST} were evaluated by Arlequin 3.5 (Excoffier and Lischer 2010) and DnaSP v5, respectively. A 95% set of plausible haplotype networks and the outgroup probability of the haplotypes were computed based on statistical parsimony using TCS 1.21 (Clement et al. 2000), and the median-joining networks were drawn with NETWORK 4.3 (Bandelt et al. 1999). To examine the relationship among populations based on distance matrices, NJ methods were used with the assistance of MEGA 5.05 (Tamura et al. 2011) software. The significance of differentiation between the populations based on pairwise F_{ST} was evaluated by conducting the exact test (Raymond and Rousset 1995) with a Markov chain length of 10,000 and 1,000 burn-in steps using Arlequin 3.5. Analysis of molecular variance (AMOVA) (Excoffier et al. 1992) was performed to examine the population structure with a statistical significance test of >10,000 permutations [input files: Appendix 3 and 4]. The gene flow estimates, genetic diversity, and theta estimates within and between groups were evaluated using DnaSP v5. The mismatch distribution with population demographic parameters was also evaluated with DnaSP v5. The neutrality tests were performed by Arlequin 3.5 based on

Tajima's *D* (Tajima 1989) and Fu's *Fs* (Fu 1997), with significance tests comparing randomly generated values based on the observed θ(S) with 10,000 repeats.

Microsatellites genotyping and summary statistics

Four microsatellite loci, ANS012, ANS122, ANS036, and ANS040 (Jung et al. 2006), were used for genotyping. Fluorescently labeled (FAM, HEX, or NED) forward primers were used for PCR amplification. PCR products were run on a 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA) and size scored using GeneMapper v4.0 Software (Applied Biosystems).

For all analyses, individuals from a single geographical location were treated as a single population. Allele frequencies were calculated with GENALEX 6 (Peakall and Smouse 2006) and other format transformations were conducted with GENALEX 6 and CONVERT (Glaubitz 2004). The mean number of alleles per locus (N_A), effective number of alleles (N_E), and observed (H_O) and expected heterozygosity (H_E) were calculated with POPGENE 1.32 (Yeh et al. 1997), and allelic richness (*AR*) was generated with FSTAT 2.9.3.2 (Goudet 2001). All microsatellite loci were tested for deviations from Hardy-Weinberg equilibrium (HWE) using POPGENE 1.32 and non-random association (linkage disequilibrium) test between loci were performed by GENEPOP (Raymond and Rousset 1995; Rousset 2008).

Population structure and Mantel test

A Bayesian clustering method was used to identify genetic clusters in the data set, implemented with STRUCTURE 2.3.3 (Pritchard et al. 2003). Five independent

runs were performed for each value of K (K = 1 to 5), with a burn-in period of 100,000 iterations, replications of 100,000, and admixture model. The most likely number of clusters was determined by calculating ΔK using STRUCTURE HARVESTER (Earl and vonHoldt 2011), and the STRUCTURE results were visualized in DISTRUCT 1.1 (Rosenberg 2004).

Pairwise R_{ST} and F_{ST} with permutations of 1,000 were calculated by Arlequin 3.5 (Excoffier and Lischer 2010). Nei's genetic distance (Nei 1972) was calculated using POPGENE 1.32, and an unweighted pair group method with arithmetic mean (UPGMA) tree was constructed using MEGA 5.05. Principal component analyses (PCA) based on Φ_{PT} and Mantel test were was conducted in GENALEX 6, and AMOVA was conducted in Arlequin 3.5 [input files: Appendix 5] with a stepwise mutation model and permutation of 10,000.

Results

Haplotypes and genetic diversity

A total 58 haplotypes from 21 locations (Figure 12) were observed among the 315 *An. sinensis* s.s. individuals, and the overall gene diversity value was 0.855 ± 0.013 (Table 9). The average guanine and cytosine (G+C) content was 3.1%. Nucleotide substitution was identified at 43 of the 210 sites, and no gaps were present. The nucleotide diversity per site (π) was 0.01053 ± 0.00053. In 21 sites, AD, ER, and GR showed the highest gene and nucleotide diversity values, and JI and NA showed the highest θ (S) and θ (π) values. The CH and TW displayed the lowest gene and nucleotide diversity values. The seven haplotypes showed the highest frequency,

containing 243 individuals, which was 77% of the total (Figure 13). The most frequent haplotype was CC05 and AD03, whereas 40 haplotypes (69%) were unique, occurring as private alleles and presenting in a single individual.

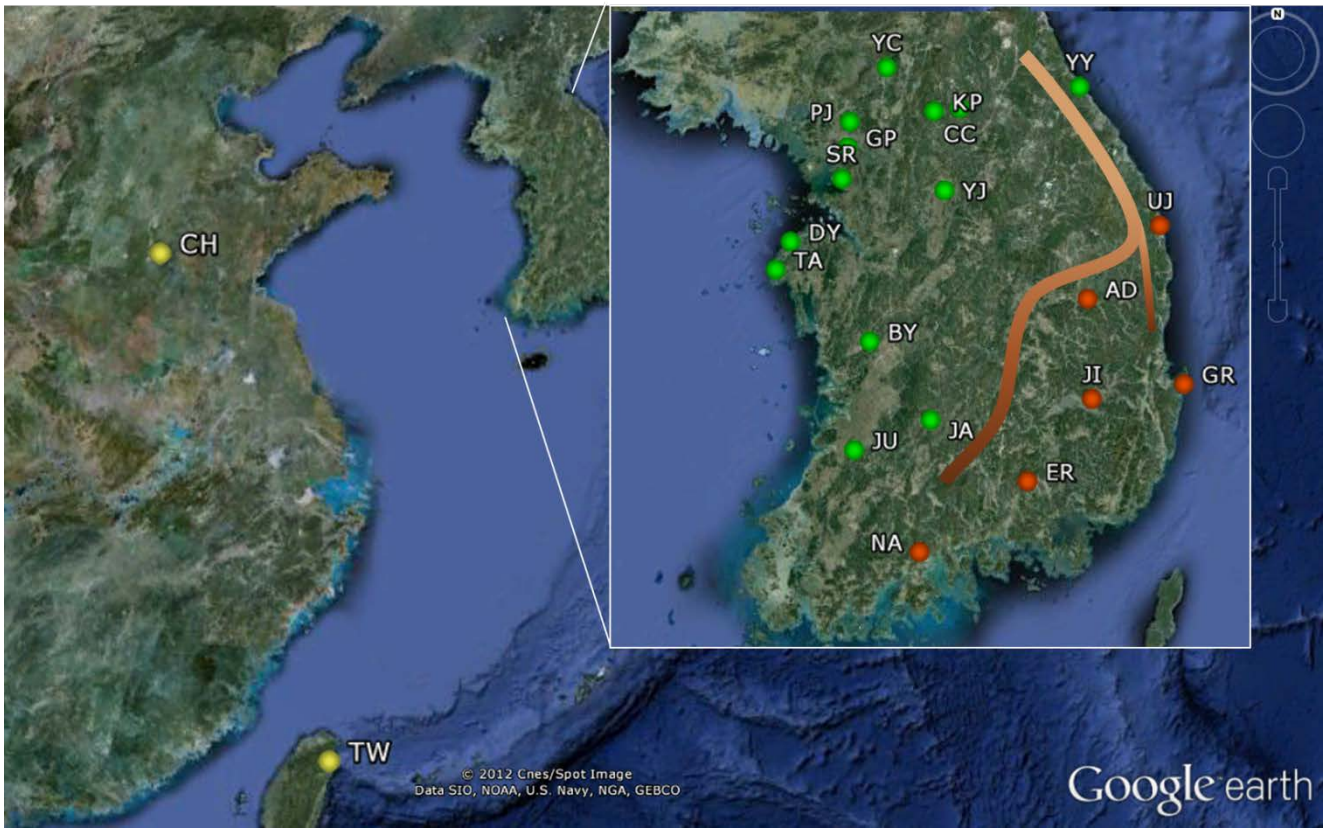

Figure 12. East Asian specimen collection locations are identified on the regional map. Names of locations are abbreviated and the full names are listed in Table 9. Populations belonging to Group 1, Group 2, and Group 3 based on mitochondrial DNA are represented as green, red, and yellow circles, respectively. The brown solid lines indicate the Taebaek and Sobaek mountain ranges.

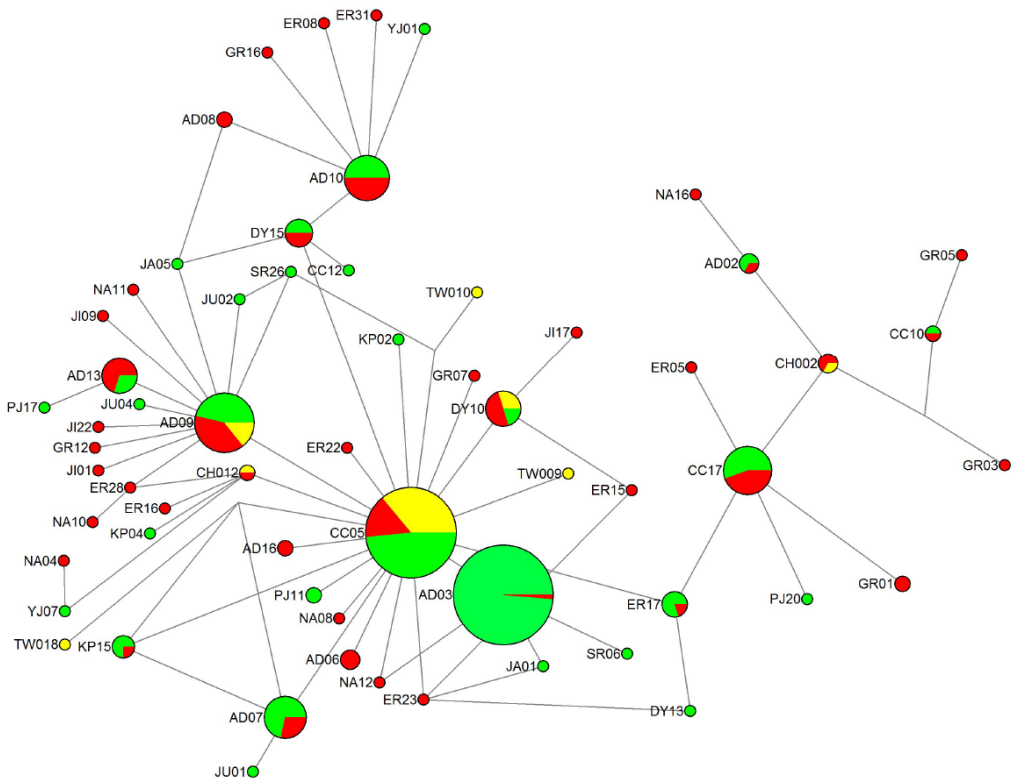

Figure 13. The 95% set of plausible haplotype networks as calculated by Network 4.6. Each circle represents a haplotype, and the numbers indicate haplotype identification. The size of a circle denotes the number of individuals that contain the haplotype, and the shaded portions of the pies indicate the group containing the particular haplotype. Group 1, Group 2, and Group 3 are represented as green, red, and yellow, respectively.

Table 9. Mitochondrial DNA-derived geographic information, indices of genetic diversity, and theta estimates for each population.

Name	Sample sites	Geographic Coordinates	Sample size	No. haplotypes	Gene diversity	Nucleotide diversity	θ(π)	θ(S)
AD	ANDONG	36° 33′ 32″ N 128° 46′ 05″ E	11	9	0.964(±0.051)	0.01420(±0.00906)	4.097(±1.937)	2.982(±1.902)
BY	BOOYEO	36° 17′ 37″ N 126° 56′ 57″ E	7	3	0.667(±0.160)	0.00771(±0.00591)	1.633(±1.032)	1.619(±1.240)
CC	CHOONCHEON	37° 51′ 06″ N 127° 43′ 08″ E	14	6	0.681(±0.132)	0.01136(±0.00737)	3.145(±1.478)	2.385(±1.548)
DY	DANYANG	36° 58′ 00″ N 126° 16′ 00″ E	17	7	0.772(±0.079)	0.00945(±0.00628)	2.662(±1.247)	1.985(±1.319)
ER	EUIRYEONG	35° 20′ 53″ N 128° 14′ 29″ E	25	17	0.963(±0.021)	0.01600(±0.00946)	4.502(±1.767)	3.360(±1.986)
GP	GIMPO	37° 35′ 41″ N 126° 45′ 58″ E	12	4	0.682(±0.102)	0.00887(±0.00614)	2.318(±1.200)	1.864(±1.290)
GR	GURYONGPO	35° 58′ 21″ N 129° 33′ 04″ E	19	12	0.942(±0.035)	0.01905(±0.01113)	4.578(±1.890)	4.000(±2.337)
JA	JINAN	35° 46′ 00″ N 127° 27′ 00″ E	19	9	0.836(±0.068)	0.01053(±0.00679)	2.575(±1.190)	2.211(±1.426)
JI	JAIN	35° 53′ 23″ N 128° 47′ 04″ E	19	12	0.936(±0.037)	0.01571(±0.00944)	4.864(±1.989)	3.298(±1.982)
JU	JEONGEUP	35° 34′ 00″ N 126° 49′ 00″ E	9	6	0.833(±0.127)	0.01455(±0.00947)	4.047(±2.010)	3.056(±1.988)
KP	KAPYEONG	37° 50′ 00″ N 127° 30′ 00″ E	16	7	0.792(±0.089)	0.01095(±0.00709)	3.315(±1.501)	2.300(±1.489)
NA	NAKAN	34° 52′ 58″ N 127° 20′ 52″ E	16	12	0.950(±0.041)	0.01480(±0.00908)	4.822(±2.047)	3.108(±1.906)
PJ	PAJOO	37° 46′ 00″ N 126° 47′ 00″ E	26	10	0.800(±0.057)	0.01225(±0.00756)	3.407(±1.399)	2.572(±1.588)
SR	SORAE	37° 23′ 00″ N 126° 43′ 00″ E	19	6	0.778(±0.072)	0.00969(±0.00636)	2.289(±1.088)	2.035(±1.336)
TA	TAEAN	36° 46′ 30″ N 126° 09′ 42″ E	13	4	0.603(±0.131)	0.00647(±0.00480)	1.611(±0.900)	1.359(±1.008)
UJ	ULJIN	37° 02′ 16″ N 129° 23′ 23″ E	10	7	0.867(±0.107)	0.01090(±0.00737)	3.181(±1.605)	2.289(±1.547)
YC	YEONCHEON	38° 08′ 00″ N 127° 06′ 00″ E	10	5	0.822(±0.097)	0.01069(±0.00725)	2.828(±1.459)	2.244(±1.523)
YJ	YEOJOO	37° 18′ 00″ N 127° 35′ 00″ E	12	6	0.849(±0.074)	0.01205(±0.00784)	3.643(±1.722)	2.530(±1.646)
YY	YANGYANG	37° 58′ 59″ N 128° 44′ 29″ E	8	5	0.857(±0.108)	0.00935(±0.00672)	2.314(±1.308)	1.964(±1.411)
CH	CHINA, Shandong Province	35° 24′ 00″ N 116° 35′ 00″ E	13	4	0.423(±0.165)	0.00611(±0.00460)	1.933(±1.029)	1.282(±0.965)
TW	TAIWAN, I-Lan County	24° 41′ 00″ N 121° 43′ 00″ E	20	5	0.505(±0.126)	0.00576(±0.00428)	1.973(±0.965)	1.211(±0.899)
Total			315	58				

Hardy-Weinberg equilibrium, linkage disequilibrium, and microsatellite polymorphism

G^2 likelihood ratio tests were performed and all 23 populations (Figure 14) were in HWE after sequential Bonferroni correction. Fisher's exact tests for linkage disequilibrium (LD) were conducted and no pair of loci appeared in random-association, suggesting no LD between loci.

Polymorphism at four microsatellite loci from all the populations varied. The summary statistics of genetic variability among populations are shown in Table 10. The greatest difference between maximum N_A in GR (8.500) and the minimum N_A in YY (3.750) was observed. The difference between maximum and minimum N_E and *AR* was smaller than N_A.

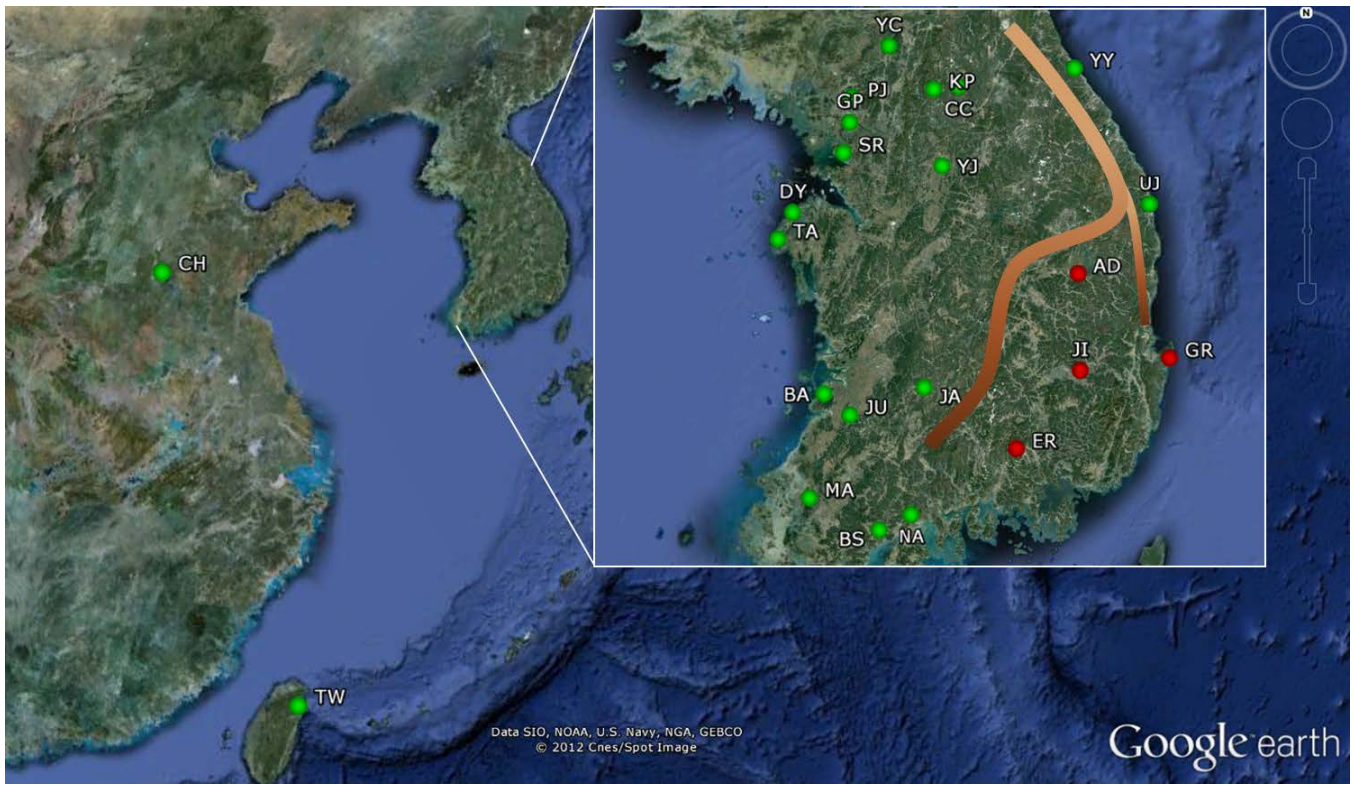

Figure 14. East Asian specimen collection locations are identified on the regional map. Names of locations are abbreviated and their full names are represented in Table 10. Populations belonging to the Group A and Group B based on microsatellites are represented as green, red circles, respectively. The brown solid line indicates the Taebaek and Sobaek mountain ranges.

Table 10. Microsatellite-derived summary of regional information and genetic variability of samples.

Name	Sample sites	Geographic Coordinates	Sample size	N_A	AR	N_E	H_O	H_E
AD	ANDONG	36° 33′ 32″ N 128° 46′ 05″ E	11	5.500	3.557	2.955	0.568	0.682
BS	BOSEONG	34° 50′ 29″ N 127° 21′ 08″ E	16	5.750	3.400	2.936	0.609	0.673
CC	CHOONCHEON	37° 51′ 06″ N 127° 43′ 08″ E	8	5.000	3.871	3.569	0.625	0.733
DY	DANYANG	36° 58′ 00″ N 126° 16′ 00″ E	15	7.000	4.029	4.072	0.583	0.718
ER	EUIRYEONG	35° 20′ 53″ N 128° 14′ 29″ E	25	7.250	3.646	3.200	0.116	0.077
GP	GIMPO	37° 35′ 41″ N 126° 45′ 58″ E	17	6.500	3.940	3.862	8.500	3.704
GR	GURYONGPO	35° 58′ 21″ N 129° 33′ 04″ E	43	8.500	3.893	3.704	0.626	0.709
JA	JINAN	35° 46′ 00″ N 127° 27′ 00″ E	11	6.750	4.037	3.307	0.636	0.719
JI	JAIN	35° 53′ 23″ N 128° 47′ 04″ E	29	7.750	3.667	3.372	0.629	0.679
JU	JEONGEUP	35° 34′ 00″ N 126° 49′ 00″ E	10	5.750	3.943	3.645	0.525	0.746
KP	KAPYEONG	37° 50′ 00″ N 127° 30′ 00″ E	14	6.000	3.727	3.329	0.589	0.696
MA	MOOAN	34° 59′ 07″ N 126° 28′ 54″ E	6	4.500	3.816	3.169	0.458	0.720
NA	NAKAN	34° 52′ 58″ N 127° 20′ 52″ E	28	8.000	3.749	3.260	0.634	0.697
PJ	PAJOO	37° 46′ 00″ N 126° 47′ 00″ E	16	6.250	3.919	3.604	0.703	0.729
SR	SORAE	37° 23′ 00″ N 126° 43′ 00″ E	24	8.250	4.003	3.905	0.740	0.737
TA	TAEAN	36° 46′ 30″ N 126° 09′ 42″ E	12	7.250	3.853	3.853	0.688	0.751
UJ	ULJIN	37° 02′ 16″ N 129° 23′ 23″ E	16	6.750	3.882	3.797	0.766	0.736
YC	YEONCHEON	38° 08′ 00″ N 127° 06′ 00″ E	9	5.500	3.885	3.458	0.694	0.724
YJ	YEOJOO	37° 18′ 00″ N 127° 35′ 00″ E	11	6.250	3.995	3.935	0.659	0.698
YY	YANGYANG	37° 58′ 59″ N 128° 44′ 29″ E	4	3.750	3.750	2.897	0.500	0.688
BA	BUAN	35° 43′ 47″ N 126° 34′ 27″ E	16	6.250	3.635	3.544	0.625	0.693
CH	CHINA, Shandong Province	35° 24′ 00″ N 116° 35′ 00″ E	13	5.500	3.495	2.683	0.496	0.653
TW	TAIWAN, I-Lan County	24° 41′ 00″ N 121° 43′ 00″ E	20	7.500	4.161	3.990	0.607	0.760

Abbreviations: N_A, number of alleles; AR, allelic richness corrected for sample size; N_E, effective number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity

Population structure and among group comparison

The pairwise F_{ST} analysis (Table 11) and the NJ analysis of pairwise F_{ST} and γ_{ST} (Figure 15) results based on mitochondrial control region data showed three separate clusters. Group 1 was comprised of 13 populations presenting in the northern region of the ROK. Group 2 was comprised of four populations found in the southern region of the ROK, and Group 3 was comprised of two populations from China (CH) and Taiwan (TW) (Figure 12). Based on the results of AMOVA (Table 12), most of the genetic variance resided within populations (87.35%), and significant variance was observed among groups (13.68%). Significant genetic differentiation among populations was not observed within groups, but the X^2 test of genetic differentiation showed positive results for genetic differentiation among the three groups (Table 13 and 14). All of the genetic diversity estimate in Group 2 were highest, followed by the Group 1 and Group 3. Members of Group 2 carried 16 of the 40 private alleles and 11 of the 40 private alleles were found in Group 3. The most frequent haplotype, AD03, included only specimens from Group 1, except one specimen from AD that came from Group 2 (Figure 13).

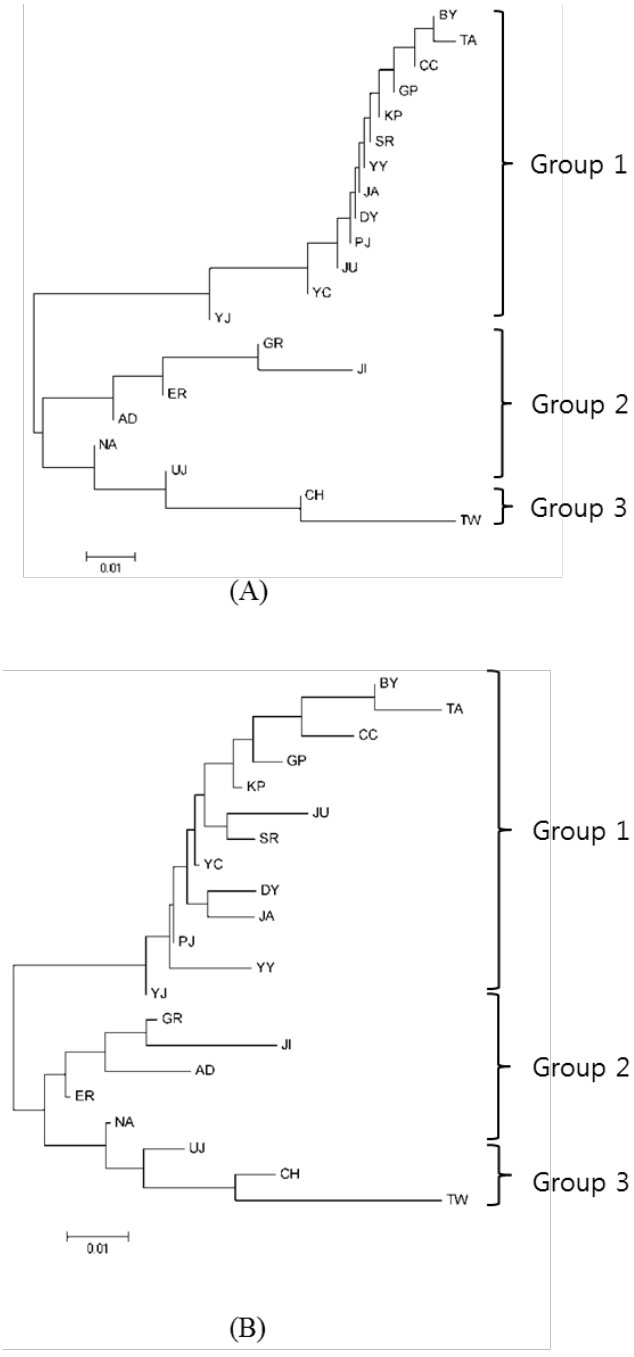

Figure 15. Mitochondrial control region-derived population trees constructed using NJ analysis of pairwise F_{ST} A and γ_{ST} B matrices.

Table 11. Mitochondrial DNA-derived pairwise F_{ST} values among populations of *An. sinensis* s.s.

	AD	BY	CC	CH	DY	ER	GP	GR	JA	JI	JU	KP	NA	PJ	SR	TA	TW	UJ	YC	YJ
BY	0.0993																			
CC	**0.1108**	0.0000																		
CH	**0.2010**	**0.2621**	**0.2822**																	
DY	**0.0916**	0.0000	0.0403	0.0711																
ER	0.0000	**0.0869**	**0.1075**	**0.1381**	**0.0602**															
GP	**0.1016**	0.0000	0.0000	**0.1759**	0.0000	**0.0878**														
GR	0.0000	0.0894	**0.0846**	**0.1350**	**0.0710**	0.0006	**0.0841**													
JA	0.0573	0.0000	0.0000	**0.2353**	0.0133	**0.0459**	0.0000	0.0588												
JI	0.0000	**0.1755**	**0.1500**	**0.1971**	**0.1282**	0.0128	**0.1366**	0.0000	**0.0903**											
JU	0.0000	0.0000	0.0000	**0.2154**	0.0214	0.0234	0.0000	0.0153	0.0000	0.0325										
KP	0.0679	0.0000	0.0000	**0.1896**	0.0000	**0.0591**	0.0000	0.0574	0.0000	**0.1124**	0.0000									
NA	0.0000	0.0718	**0.1027**	**0.1075**	0.0308	0.0000	**0.0679**	0.0190	0.0478	0.0316	0.0111	0.0399								
PJ	0.0362	0.0000	0.0051	**0.1012**	0.0000	**0.0425**	0.0000	0.0426	0.0000	**0.0848**	0.0000	0.0000	0.0255							
SR	**0.0706**	0.0000	0.0000	**0.2029**	0.0010	**0.0770**	0.0000	**0.0737**	0.0000	**0.1020**	0.0000	0.0000	**0.0587**	0.0000						
TA	**0.1486**	0.0000	0.0000	**0.3154**	0.0360	**0.1335**	0.0000	**0.1427**	0.0223	**0.2082**	0.0055	0.0000	**0.1225**	0.0048	0.0000					
TW	**0.2465**	0.2550	**0.3060**	0.0000	**0.0826**	**0.1683**	**0.1941**	**0.1984**	**0.2548**	**0.2595**	**0.2573**	**0.2131**	**0.1265**	**0.1286**	**0.2269**	**0.3077**				
UJ	0.0093	**0.0731**	**0.1197**	0.0282	0.0000	0.0000	0.0655	0.0115	0.0739	0.0779	0.0513	0.0389	0.0000	0.0026	0.0808	**0.1533**	0.0650			
YC	0.0000	0.0000	0.0000	**0.1767**	0.0000	0.0101	0.0000	0.0085	0.0000	0.0533	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	**0.2056**	0.0059		
YJ	0.0094	0.0000	0.0000	**0.1208**	0.0000	0.0147	0.0000	0.0239	0.0000	0.0677	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	**0.1514**	0.0000	0.0000	
YY	0.0164	0.0000	0.0000	**0.1757**	0.0000	0.0246	0.0000	0.0441	0.0000	**0.1037**	0.0000	0.0000	0.0044	0.0000	0.0000	0.0000	**0.1772**	0.0000	0.0000	0.0000

Significant values are in bold. Negative values are represented as zero

Table 12. Mitochondrial DNA-derived AMOVA of geographic variation among the *An. sinensis* s.s. individuals.

	Source of variation	df	Sum of squares	Variance components	Percentage of variance (%)	F-index
Three Groups	Among groups	2	11.499	0.06222	13.68	**0.13683
	Among populations within groups	18	5.915	-0.00025	-1.03	-0.01193
	Within populations	294	116.771	0.39718	87.35	**0.12654
	Total	314	134.184	0.45472		
Group 1 vs. Group 2 and 3	Among groups	1	7.246	0.04353	9.67	**0.09672
	Among populations within groups	19	10.167	0.00932	2.07	*0.02294
	Within populations	294	116.771	0.39718	88.35	**0.11744
	Total	314	134.184	0.45003		
Group 2 vs. Group 1 and 3	Among groups	1	5.32	0.03398	7.59	**0.07595
	Among populations within groups	19	12.094	0.01620	3.62	**0.03919
	Within populations	294	116.771	0.39718	88.78	**0.11217
	Total	314	134.184	0.44736		
Group 3 vs. Group 1 and 2	Among groups	1	5.371	0.07953	16.14	**0.16141
	Among populations within groups	19	12.042	0.01600	3.25	**0.03872
	Within populations	294	116.771	0.39718	80.61	**0.19388
	Total	314	134.184	0.49270		

* $0.0001 < P < 0.001$; ** $0.001 < P < 0.01$.

df, degrees of freedom.

Table 13. Mitochondrial DNA-derived comparison of estimated gene flow, genetic diversity, and neutrality tests in Group 1, Group 2, and Group 3 of *An. sinensis* s.s.

		Group 1	Group 2	Group 3
P-value of genetic differentiation		0.3982	0.5032	0.3677
Hudson and others (1992)	F_{ST}	-0.0264	-0.0034	-0.0085
	N_m	-9.7	-74.3	-29.76
Number of individuals		182	100	33
Number of haplotypes		29	42	7
Haplotype diversity		0.783	0.952	0.47
Nucleotide diversity	(π)	0.009	0.015	0.004
Theta Estimates	$\theta(\pi)$	0.0214	0.0350	0.0119
	θ(S)	0.0214	0.0331	0.0119
Neutrality Tests	Tajima's *D*	-1.613	*-1.787	*-2.064
	Fu's F_s	**-20.707	**-40.306	*-3.2940
	Fu and Li's *D**	-2.3138	**-3.4900	*-3.0181
	Fu and Li's *F**	*-2.4411	**-3.3715	*-3.1872

*0.01< *P* < 0.05; **P < 0.01.

Table 14. Mitochondrial DNA-derived genetic differentiation and F_{ST} values between the groups.

	Group 1-Group 2	Group 2-Group 3	Group 1-Group 3
P-value of genetic differentiation	0	0	0
Population pairwise F_{ST}	0.0960	0.0569	0.1082
P-value of F_{ST}	0	0.0447	0

After comparing pairwise population F_{ST} and R_{ST} values and *P*-values calculated from permutation tests (Table 15), the microsatellite genetic difference among populations showed similar results with a previous population genetic study in *An. sinensis* s.s. using mitochondrial control regions (Jung et al. 2007). A UPGMA tree generated by pairwise F_{ST} values distinguished two groups of populations (Figure 16). One group included AD, GR, ER, and JI from the southern part of the peninsula and the other group included rest of the populations. The Bayesian analysis of population structure also indicated that the most likely number of clusters was two when evaluated in terms of ΔK (Figure 17). A PCA of all populations based on the Φ_{PT} matrix recovered the same two genetic groups as the Bayesian analysis (Figure 18). AMOVA results showed that most of the genetic variance existed within populations (86.60 %, $P < 0.001$) (Table 16). Significant variance was observed among groups (9.61% $P < 0.001$) and overall genetic differentiation between two clusters was moderate ($F_{ST} = 0.134$, $P < 0.001$). Of the four loci, ANS012, ANS122, ANS036, and ANS040, ANS012 showed the highest F_{CT} =0.364 (P=0.0000), indicating that this locus has significantly contributed the genetic divergence between the two groups (Table 17).

Table 15. Microsatellite-derived matrix of pairwise R_{ST} (lower diagonal) and F_{ST} (upper diagonal)

	*AD	BS	CC	DY	*ER	GP	*GR	JA	*JI	*JU	KP	MA	NA	PJ	SR	TA	UJ	YC	YJ	YY	BA	CH	TW
*AD	-	**0.091**	0.020	**0.063**	0.019	**0.070**	0.012	**0.065**	0.027	0.023	**0.072**	**0.118**	**0.053**	**0.050**	**0.068**	**0.049**	**0.027**	0.035	**0.078**	**0.106**	**0.081**	**0.126**	**0.123**
BS	**0.165**	-	0.017	**0.069**	**0.087**	**0.062**	**0.101**	**0.073**	**0.095**	0.028	**0.071**	**0.072**	0.009	**0.055**	0.003	0.007	0.005	**0.045**	**0.039**	0.023	**0.079**	**0.080**	**0.085**
CC	**0.219**	0.000	-	**0.050**	**0.060**	**0.055**	**0.046**	**0.074**	**0.058**	0.014	0.017	0.062	0.027	0.033	0.008	0.009	0.000	0.000	0.026	0.004	**0.059**	**0.089**	**0.065**
DY	**0.116**	0.000	0.000	-	**0.075**	0.012	**0.052**	0.013	**0.047**	0.004	**0.037**	**0.073**	**0.062**	0.012	0.010	0.008	0.011	**0.047**	0.000	**0.083**	0.025	**0.058**	**0.059**
*ER	0.000	**0.109**	**0.132**	**0.080**	-	**0.094**	0.014	**0.059**	0.014	0.021	**0.109**	**0.119**	**0.061**	**0.080**	**0.078**	**0.067**	**0.034**	**0.070**	**0.093**	**0.143**	**0.099**	**0.152**	**0.137**
GP	0.065	0.027	0.099	0.017	**0.078**	-	**0.080**	0.000	**0.082**	0.025	**0.037**	0.036	**0.034**	0.004	**0.017**	0.000	**0.019**	**0.042**	0.018	**0.082**	**0.036**	0.020	**0.033**
*GR	0.038	**0.075**	0.066	**0.054**	0.002	**0.099**	-	**0.056**	0.009	0.012	**0.106**	**0.124**	**0.076**	**0.069**	**0.072**	**0.068**	**0.039**	**0.066**	**0.070**	**0.143**	**0.082**	**0.144**	**0.130**
JA	0.027	0.032	0.041	0.020	0.001	0.015	0.052	-	**0.063**	0.018	**0.054**	0.016	0.028	0.004	**0.034**	0.005	0.017	**0.050**	0.036	**0.120**	**0.043**	**0.049**	**0.058**
*JI	0.009	**0.114**	**0.119**	**0.085**	0.000	**0.105**	0.000	**0.066**	-	0.000	**0.101**	**0.133**	**0.076**	**0.089**	**0.070**	**0.067**	**0.036**	**0.065**	**0.048**	**0.123**	**0.083**	**0.128**	**0.126**
*JU	0.056	0.087	0.039	0.072	0.013	**0.095**	0.078	0.000	0.076	-	0.045	0.066	0.018	0.025	0.010	0.002	0.000	0.023	0.000	0.043	0.037	**0.062**	**0.072**
KP	**0.213**	0.063	0.115	0.057	**0.181**	0.031	**0.187**	0.023	**0.221**	0.082	-	0.064	**0.050**	0.012	**0.022**	0.009	0.008	0.023	0.027	0.023	**0.059**	**0.022**	**0.040**
MA	0.052	0.054	0.154	0.023	0.035	0.000	0.068	0.000	0.086	**0.013**	0.022	-	**0.055**	0.044	**0.058**	0.032	**0.044**	0.062	**0.060**	0.095	**0.087**	**0.093**	**0.063**
NA	0.053	**0.117**	**0.208**	**0.097**	**0.079**	0.011	**0.130**	0.011	**0.133**	**0.131**	**0.087**	0.000	-	**0.027**	**0.021**	0.000	**0.008**	**0.035**	0.050	0.034	**0.060**	**0.039**	**0.068**
PJ	**0.183**	**0.101**	**0.200**	**0.085**	**0.170**	0.014	**0.186**	0.017	**0.219**	**0.122**	0.009	0.000	0.023	-	0.015	0.000	0.009	**0.043**	0.027	0.061	**0.035**	**0.037**	**0.050**
SR	**0.197**	0.000	0.000	0.000	**0.147**	**0.044**	**0.112**	**0.053**	**0.157**	**0.120**	0.046	0.062	**0.136**	**0.091**	-	0.000	0.000	0.013	0.000	0.025	**0.035**	**0.029**	**0.038**
TA	**0.138**	**0.080**	**0.160**	0.065	**0.141**	0.000	**0.167**	0.006	**0.191**	0.097	0.003	0.000	0.008	0.000	**0.078**	-	0.000	0.005	0.000	0.020	0.008	0.007	0.028
UJ	**0.116**	0.000	0.000	0.000	**0.077**	0.019	**0.055**	0.016	**0.085**	0.063	0.049	0.019	**0.098**	**0.085**	0.000	0.067	-	0.000	0.002	0.031	**0.033**	**0.043**	**0.049**
YC	**0.149**	0.098	0.185	0.076	**0.143**	0.000	**0.169**	0.000	**0.194**	0.069	0.000	0.000	0.004	0.000	0.090	0.000	0.073	-	0.039	0.050	0.039	0.037	**0.056**
YJ	**0.107**	0.000	0.000	0.000	**0.082**	0.014	**0.055**	0.040	**0.073**	0.069	0.081	0.054	**0.114**	**0.118**	0.000	**0.087**	0.000	**0.102**	-	0.026	0.029	**0.044**	**0.046**
YY	0.150	0.134	0.222	0.089	0.131	0.002	0.163	0.000	**0.195**	0.010	0.000	0.000	0.000	0.000	0.114	0.000	0.083	0.000	**0.131**	-	**0.092**	0.055	0.057
BA	**0.216**	**0.204**	**0.284**	**0.180**	**0.233**	**0.074**	**0.267**	**0.060**	**0.287**	**0.150**	0.051	0.049	**0.059**	0.008	**0.192**	0.000	**0.177**	0.000	**0.199**	0.000	-	**0.077**	**0.074**
CH	0.069	**0.091**	0.080	**0.076**	**0.094**	0.062	**0.151**	0.000	**0.159**	0.045	0.036	0.000	0.052	0.018	**0.109**	0.009	**0.080**	0.000	**0.088**	0.000	0.011	-	0.018
TW	**0.301**	**0.124**	**0.230**	**0.113**	**0.258**	**0.051**	**0.248**	**0.075**	**0.296**	**0.179**	0.000	**0.092**	**0.102**	0.000	**0.091**	0.000	**0.110**	0.000	**0.148**	0.001	0.025	0.056	-

Significant values ($P < 0.05$) are with boldface and underlined values are still significant after Bonferroni correction; *, locations belonging to Group B

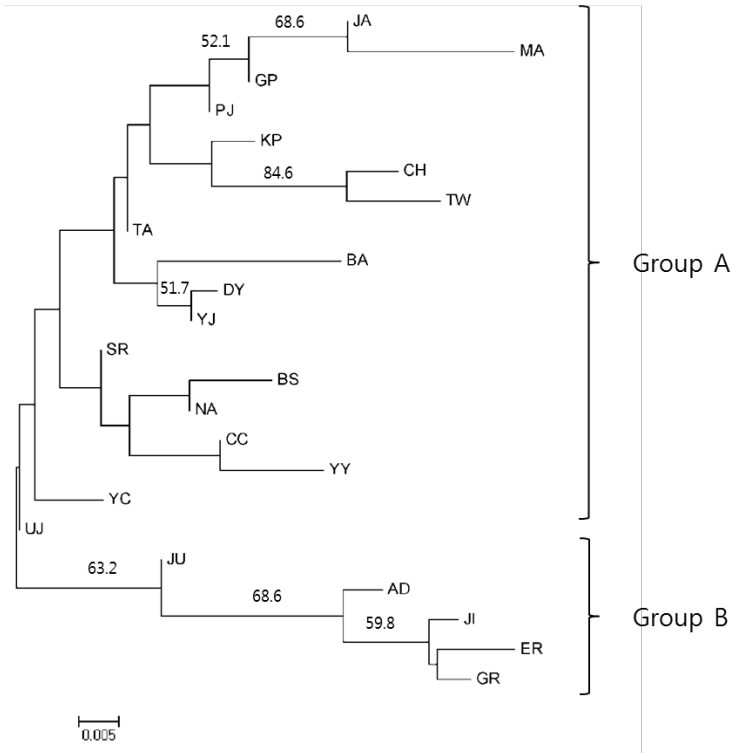

Figure 16. A microsatellite-derived UPGMA tree depicting the genetic relationship among the local populations inferred from Nei's distance. The numbers on the nodes represent the bootstrapping confidence values and values of <50% have been hidden. The Nei's distance values are proportional to branch lengths (see scale bar).

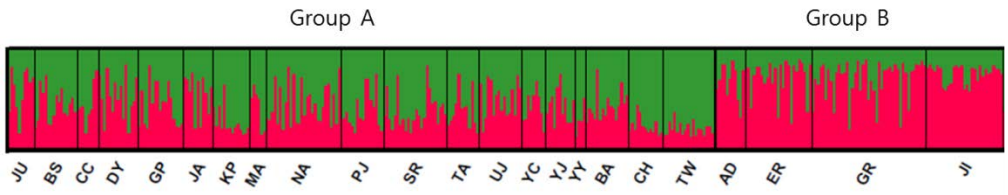

Figure 17. A bar plot denoting estimated population structure using STRUCTURE 2.5 based on allele frequency data (*K*=2).

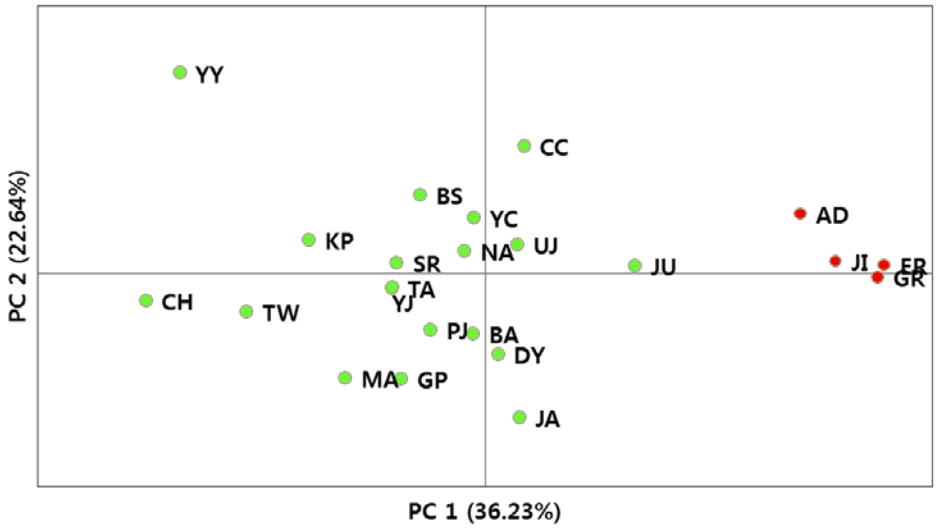

Figure 18. A plot representing results of principal components analysis of molecular variance executed with GENALEX 6.2, using the Φ_{PT} pairwise distance matrix. The first two components account for 58.87% of the total variation. Populations belonging to Group A and Group B are represented as green and red circles, respectively.

Table 16. Microsatellite-derived AMOVA of geographic variation among the *An. sinensis* s.s. individuals.

Source of variation	df	Sum of squares	Variance components	Percentage of variance (%)	F-index
Among groups	1	5218.828	14.81024	9.61	**0.0961**
Among populations within groups	21	6624.525	5.83534	3.79	0.0419
Within populations	725	96769.763	133.47554	86.60	**0.1340**
Total	747	108613.116	154.12111		

Bold F-index represents $0.001 < P < 0.01$.
df, degree of freedom

Table 17. Microsatellite-derived results of locus-by-locus AMOVA of two groups.

Locus	Percentage of variation			Fixation indices					
	Among groups	Among populations	Within populations	F_{SC}	*P*-value	F_{ST}	*P*-value	F_{CT}	*P*-value
ANS012	36.42	2.59	60.99	0.041	0.003	0.390	0	0.364	0
ANS122	2.15	7.52	90.33	0.077	0	0.097	0	0.021	0.143
ANS036	2.10	1.66	96.23	0.017	0.301	0.038	0.254	0.021	0.032
ANS040	-0.74	2.36	98.31	0.023	0.477	0.017	0.423	-0.007	0.753

Population expansion and isolation by distance

The mismatch distribution of pairwise nucleotide differences among mitochondrial control region sequences among all groups was smooth and unimodal (Figure 19). The three groups had recently experienced expansion according to the mismatch analysis (Table 18). The smallest θ_0 value and the largest τ value were observed in Group 2, indicating that this group may have experienced population expansion earlier with a smaller initial population size than the other groups.

Table 18. Mismatch distribution estimates in Group 1, Group 2, and Group 3 of *An. sinensis* s.s.

		Group 1	Group 2	Group 3
Mismatch Distribution	θ_0	0.658	0.254	0.733
	τ	1.254	2.870	0.093
	Raggedness	0.0135	0.0226	0.1016

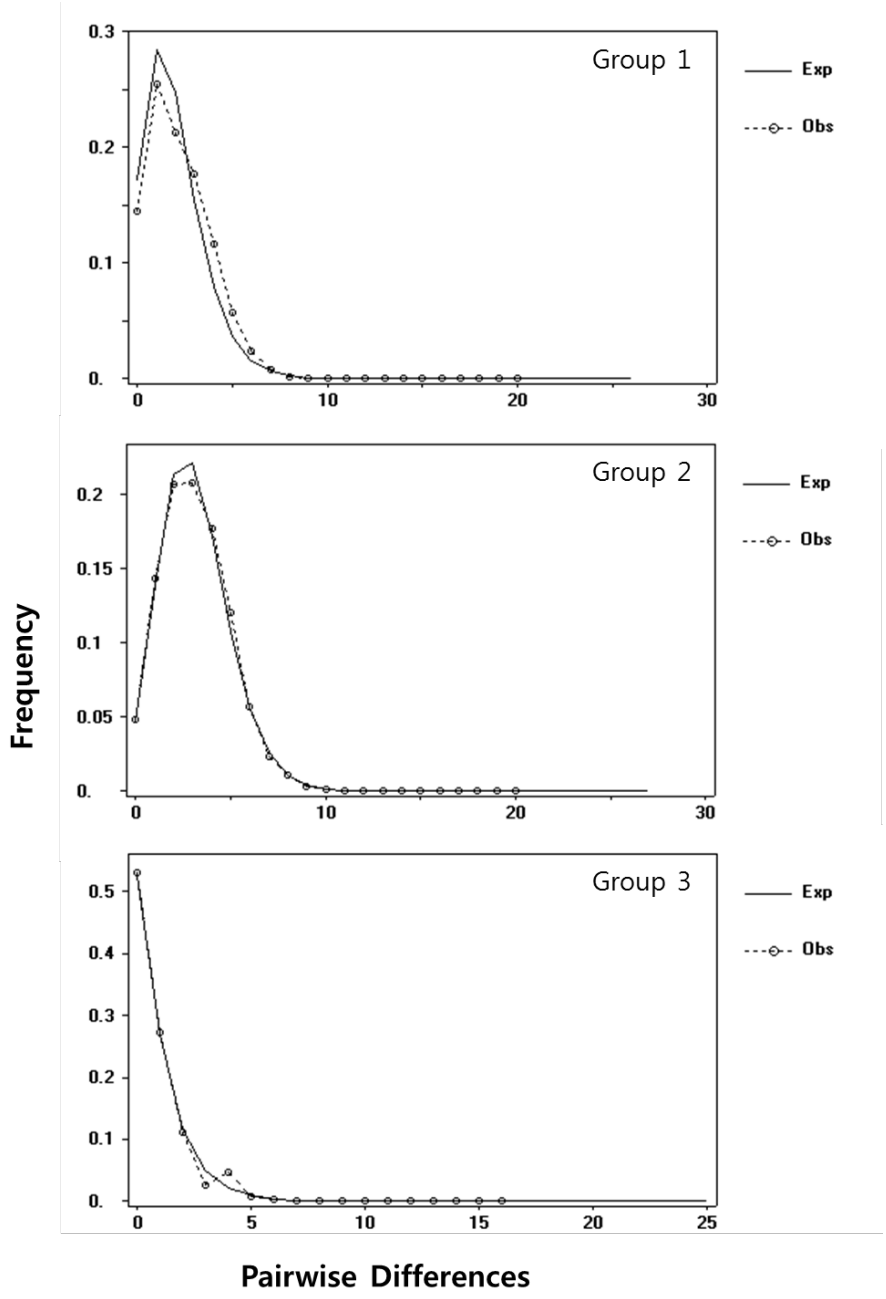

Figure 19. Mismatch distribution in East Asia in all of the individuals from Group 1, Group 2, and Group 3 based on the mitochondrial control region. The expected values (solid line) were estimated according to the sudden expansion model.

The Mantel regression for mitochondrial DNA revealed isolation by distance (Figure 20). A highly positive and statistically significant relationship was observed among all the populations ($y = 0.0001x + 0.0209$, $R^2 = 0.3251$, $P = 0.001$) and moderately positive and statistically significant relationships were observed among Korean populations ($y = 0.0001x + 0.0066$, $R^2 = 0.064$, $P = 0.009$). The results of Mantel tests based on microsatellites did not suggest a significant relationship between genetic and geographic distance (Mantel probability $P = 0.208$).

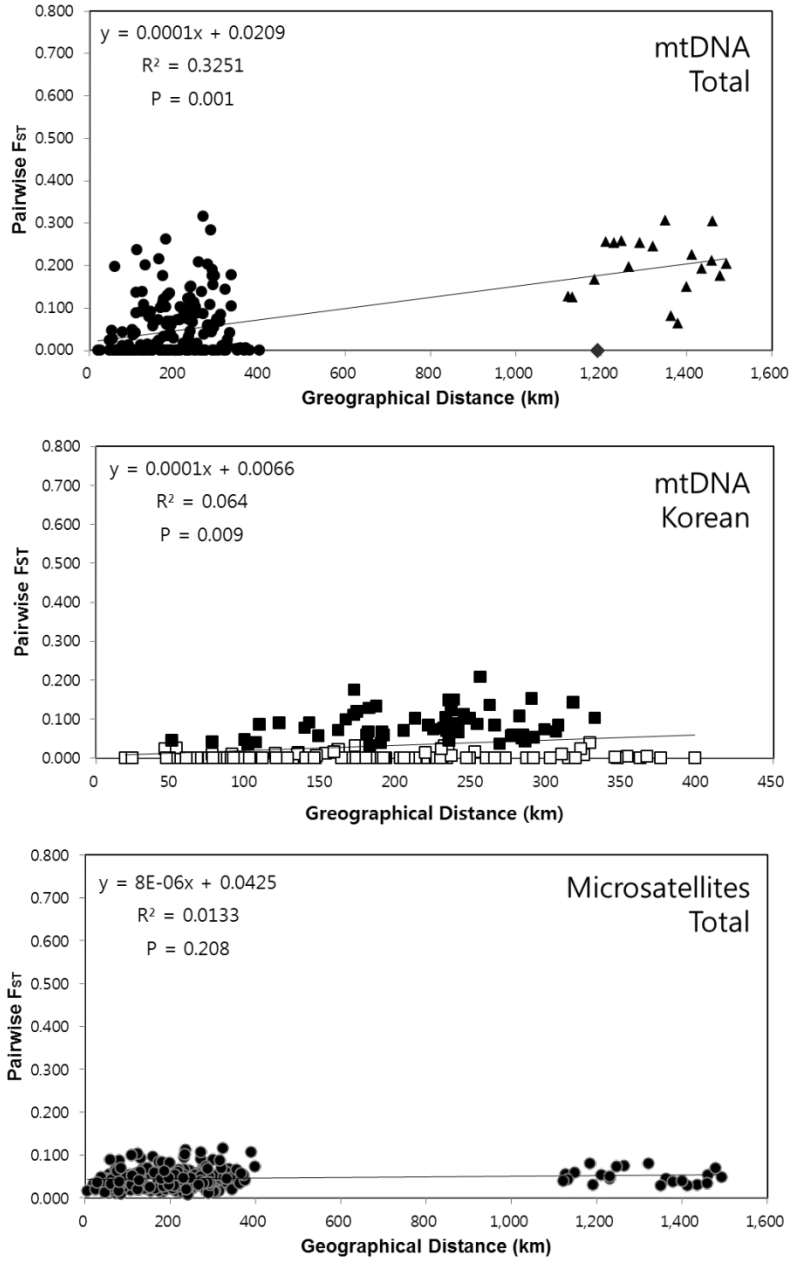

Figure 20. Mantel tests for isolation by distance. Top panel: Circles represent comparisons within Korean populations. Triangles represent comparisons between Korean populations and CH and TW. Diamonds represent comparison between CH and TW. Middle panel: Black squares represent comparison between Group 1 and Group 2 and white squares represent within-group comparison.

Discussion

Patterns of variation in mitochondrial DNA from *An. sinensis* s.s. in East Asia revealed an almost panmictic population structure, except for the distinct subdivision into three groups (Group 1, Group 2, and Group 3). Within the ROK, a population subdivision between Group 1 and Group 2 caused by mountain ranges was previously reported by Jung et al. (Jung et al. 2007). Mantel test within Korean populations showed very small but positive and significant correlation between genetic divergence and geographical distance. However, this was not caused by isolation-by-distance, but by a genetic barrier between the groups. Overall population comparison showed more positive and significant correlations, and the Korean populations (Group 1 and Group 2) were moderately diverged from the CH and TW representatives (Group 3). Since the CH and TW mosquitoes are geographically separated by about 1,200 km, and both populations exhibited 0 pairwise F_{ST} values, the subdivision of Group 3 from Group 1 and Group 2 may due to restricted gene flow (ocean in this case) in the present or past unstable demographic history. Population expansion tests were performed to examine the past demographic history and the results indicated that Group 3 underwent the most recent population expansion event compared to the other 2 groups. Thus, genetic cohesiveness observed in mitochondrial DNA within the current population implies that genetically homogenized populations of *An. sinensis* s.s. in East Asia experienced expansion rather than extensive gene flow.

The population structure based on mitochondrial DNA did not exactly

match the results carried out with microsatellites. First, the microsatellite diversity results sorted the populations into just two groups (Group A and Group B). The populations of Group 2 are similar to the populations of Group B and the population of Group A is comprised of populations from Group 1 and Group 3. Second, the pairwise F_{ST} differences between Group A and Group B were smaller than Group 1 + Group 3 and Group 2. These conflicting results may reflect the difference of inheritance and evolutionary histories in mitochondrial DNA and nuclear DNA, which can affect estimates of gene flow (Presa et al. 2002). Third, there were no positive correlations between genetic divergence and geographical distance. In general, contemporary gene flow among *Anopheles* populations must be assessed by microsatellite markers because due to their high mutation rate, these markers can detect differentiation even in weakly structured species (Temu et al. 2004; Scarpassa and Conn 2007; Czeher et al. 2010; Muturi et al. 2010). Whereas mitochondrial DNA can detect large-scale geographic differences because of maternal inheritance, the effective population size of mitochondrial DNA is only a quarter that of nuclear DNA and displays a faster genetic divergence compared with nuclear DNA (Avise 2000), and genetic drift may produce a spatial differentiation signal (Chen et al. 2004; Jung et al. 2007; O'Loughlin et al. 2007; Loaiza et al. 2011). Thus, the discrepancy between mitochondrial DNA and microsatellite-derived population structures results from the fact that after recent expansion mitochondrial DNA diverged rapidly among populations due to small effective population size, whereas microsatellites do not or only partly reflect the presence of genetically isolated

populations. Even so, the ocean as a physical barrier is not fully supported. Thus, regarding the effects of physical barriers, more extensive sampling along barrier ranges is still needed to achieve adequate resolution (Donnelly et al. 2001; Donnelly et al. 2003; Lehmann et al. 2003; Dusfour et al. 2004; Michel et al. 2005; Crawford and Lazzaro 2010; Loaiza et al. 2010; Morgan et al. 2010; Pedro et al. 2010; Vicente et al. 2011; Zarowiecki et al. 2011). Otherwise, the genetic differentiation caused by sampling gaps could be misinterpreted as a genetic barrier.

In summary, the role of the mountain ranges as a physical barrier in East Asia was well supported by both mitochondrial DNA and microsatellites. In consideration of the fact that *An. sinensis* mosquitoes use rice paddies for a spawning ground (Kim et al. 2009; Klein et al. 2009), mountain ranges may function as geographical barriers between regions and produce restricted gene flow patterns within a few hundred kilometers within the ROK. This implies that structured populations could limit the migration of important vector control genes, such as insecticide resistance and *Plasmodium* immunity among potential malaria vectors within these regions.

CONCLUSION

Understanding genetic diversity, population structure, population dynamics, and geographical distribution of vector species provides insights into dispersal potential and disease patterns. Genes and genomes undergo diversification during evolution, and a combination of diverse molecular markers and various analytical tools allows investigation of vector biology in manifold species levels.

Phylogenetic inference for the Korean malaria mosquito *Anopheles* Hyrcanus group and introgression between *An. sinensis* s.s. and *An. kleini* using a multilocus approach determined on the species level that *An. sinensis* s.s. and *An. belenrae* are more closely related to each other than to *An. kleini*, and there has been asymmetric introgression from *An. kleini* to *An. sinensis* s.s.

From the insecticide resistance studies using a non-neutral nuclear DNA marker, the finding that the highly polymorphic *kdr* gene was only observed in *An. sinensis* s.s., one out of the six *Anopheles* species studied, along with the geographical distribution recorded, suggested that there are different selection pressures on the gene depending on species, and future studies should focus on insecticide resistance monitoring and investigations of species-specific resistance mechanisms in order to maintain successful malaria vector control programs in the ROK.

Within-species genetic structure studies on *An. sinensis* s.s. using two different molecular markers showed somewhat congruent results regarding the

influence of the Sobaek and Taebaek mountain range as a genetic barrier within Korea.

Further in-depth experiments are needed to prove the current epidemiological and evolutionary dynamics of malaria vectors in the ROK, and these efforts will also serve as one of the prerequisite steps for establishing effective long-term vector control strategies in the ROK. The results should also promote national health and reduce the economic burden of malaria management through effective vector control within established management boundaries in the ROK, and they could also serve as a model case for the study of malaria epidemiology as well as other vector-mediated disease such as dengue, Japanese encephalitis, and so on.

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국문초록

말라리아의 방역을 위해서는 무엇보다도 인간에게 말라리아를 직접적으로 전달하는 매개모기에 대한 유전적 다양성, 집단 동태, 집단 구조, 집단의 지리적 분포 범위에 대한 연구가 되어야 질병의 전염경로를 파악할 수 있으며 이로서 효율적인 방제가 가능하다. DNA 분석을 통한 계통지리 및 개체군유전학적 연구를 통해 이러한 연구가 가능하다. 국내에서 말라리아를 매개하는 히르카누스 그룹 모기의 계통학, 유전적 다양도, 유전자 이입, 집단 구조 등을 보기 위해 다좌위 유전자 마커가 사용되었다. 국내 말라리아모기 6 종에 대한 계통학적 연구 결과 두 개의 clade ((*Anopheles sinensis* sensu stricto + *Anopheles belenrae*) 와 *Anopheles kleini*)를 확인하였다. *An. sinensis s.s.* 와 *An. kleini* 의 유전적 다양도와 유전자 이입에 대해 분석한 결과 *An. kleini* 로부터 *An. sinensis* s.s.로 향하는 유전자 이입이 관찰되었다. 다음으로 국내 말라리아모기에 6 종에 대한 살충제저항성 유전자의 돌연변이여부와 대립유전자의 빈도에 대해 연구한 결과 6 종 중 *An. sinensis* s.s. 한 종에서만 저항성 유전자를 발견하였으며 높은 다형성과 전국적으로 높은 빈도의 돌연변이 빈도를 보이고 있음을 밝혔다. 마지막으로 미토콘드리아 DNA 마커와 마이크로새틀라이트 마커를 이용한 동아시아에 분포하는 *An. sinensis* s.s.의 집단 구조 연구 결과, 국내의 소백산맥과 태백산맥이 유전적 장벽으로 중요한 역할을 하고 있음을 밝혔다.

주요어: 말라리아 매개 모기, 히르카누스 그룹, 집단 유전학적 구조, 계통학, 다좌위 분석, 살충제 저항성

학번: 2006-22932

APPENDIX

Appendix 1. Input file for BEAST

```
<?xml version="1.0" standalone="yes"?>

<!-- Generated by BEAUTi v1.7.1                                          -->
<!--       by Alexei J. Drummond, Andrew Rambaut and Marc A. Suchard     -->
<!--       Department of Computer Science, University of Auckland and    -->
<!--       Institute of Evolutionary Biology, University of Edinburgh    -->
<!--       David Geffen School of Medicine, University of California, Los Angeles-->
<!--       http://beast.bio.ed.ac.uk/                                    -->
<beast>

        <!-- The list of taxa to be analysed (can also include dates/ages).     -->
        <!-- ntax=101                                                          -->
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                <taxon id="L_S7-18-2"/>
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                <taxon id="SR_YY026-2"/>
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        <taxon idref="P_YC070"/>
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```

```
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                </sequence>
        </alignment>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=104                                                      -->
        <patterns id="phased_1433.patterns" from="1">
                <alignment idref="alignment1"/>
        </patterns>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=66                                                       -->
        <patterns id="aligned_COI.patterns" from="1">
                <alignment idref="alignment2"/>
        </patterns>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=55                                                       -->
        <patterns id="aligned_COII.patterns" from="1">
                <alignment idref="alignment3"/>
        </patterns>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=82                                                       -->
        <patterns id="phased_DNAJ.patterns" from="1">
                <alignment idref="alignment4"/>
        </patterns>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=269                                                      -->
        <patterns id="Its2.patterns" from="1">
                <alignment idref="alignment5"/>
        </patterns>

        <!-- The unique patterns from 1 to end                                  -->
        <!-- npatterns=137                                                      -->
        <patterns id="phased_RpL14.patterns" from="1">
                <alignment idref="alignment6"/>
        </patterns>

        <!-- A prior assumption that the population size has remained constant  -->

        <!-- throughout the time spanned by the genealogy.                      -->
        <constantSize id="constant" units="substitutions">
                <populationSize>
                        <parameter id="constant.popSize" value="0.084" lower="0.0"/>
```

```
		</populationSize>
</constantSize>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="phased_1433.startingTree" rootHeight="0.069">
		<taxa idref="phased_1433.taxa"/>
		<constantSize idref="constant"/>
</coalescentTree>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="aligned_COI.startingTree" rootHeight="2.0">
		<taxa idref="aligned_COI.taxa"/>
		<constantSize idref="constant"/>
</coalescentTree>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="aligned_COII.startingTree" rootHeight="1.8">
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		<constantSize idref="constant"/>
</coalescentTree>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="phased_DNAJ.startingTree" rootHeight="0.048">
		<taxa idref="phased_DNAJ.taxa"/>
		<constantSize idref="constant"/>
</coalescentTree>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="Its2.startingTree" rootHeight="0.2">
		<taxa idref="Its2.taxa"/>
		<constantSize idref="constant"/>
</coalescentTree>

<!-- Generate a random starting tree under the coalescent process 	-->
<coalescentTree id="phased_RpL14.startingTree" rootHeight="0.09">
		<taxa idref="phased_RpL14.taxa"/>
		<constantSize idref="constant"/>
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<!-- Generate a tree model 	-->
<treeModel id="phased_1433.treeModel">
		<coalescentTree idref="phased_1433.startingTree"/>
		<rootHeight>
			<parameter id="phased_1433.treeModel.rootHeight"/>
		</rootHeight>
		<nodeHeights internalNodes="true">
			<parameter id="phased_1433.treeModel.internalNodeHeights"/>
		</nodeHeights>
		<nodeHeights internalNodes="true" rootNode="true">
			<parameter id="phased_1433.treeModel.allInternalNodeHeights"/>
		</nodeHeights>
</treeModel>

<!-- Generate a tree model 	-->
<treeModel id="aligned_COI.treeModel">
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```

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		</nodeHeights>
		<nodeHeights internalNodes="true" rootNode="true">
			<parameter id="aligned_COI.treeModel.allInternalNodeHeights"/>
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</treeModel>

<!-- Generate a tree model                                                  -->
<treeModel id="aligned_COII.treeModel">
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			<parameter id="aligned_COII.treeModel.rootHeight"/>
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		<nodeHeights internalNodes="true" rootNode="true">
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</treeModel>

<!-- Generate a tree model                                                  -->
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		<coalescentTree idref="phased_DNAJ.startingTree"/>
		<rootHeight>
			<parameter id="phased_DNAJ.treeModel.rootHeight"/>
		</rootHeight>
		<nodeHeights internalNodes="true">
			<parameter id="phased_DNAJ.treeModel.internalNodeHeights"/>
		</nodeHeights>
		<nodeHeights internalNodes="true" rootNode="true">
			<parameter id="phased_DNAJ.treeModel.allInternalNodeHeights"/>
		</nodeHeights>
</treeModel>

<!-- Generate a tree model                                                  -->
<treeModel id="Its2.treeModel">
		<coalescentTree idref="Its2.startingTree"/>
		<rootHeight>
			<parameter id="Its2.treeModel.rootHeight"/>
		</rootHeight>
		<nodeHeights internalNodes="true">
			<parameter id="Its2.treeModel.internalNodeHeights"/>
		</nodeHeights>
		<nodeHeights internalNodes="true" rootNode="true">
			<parameter id="Its2.treeModel.allInternalNodeHeights"/>
		</nodeHeights>
</treeModel>

<!-- Generate a tree model                                                  -->
<treeModel id="phased_RpL14.treeModel">
		<coalescentTree idref="phased_RpL14.startingTree"/>
		<rootHeight>
			<parameter id="phased_RpL14.treeModel.rootHeight"/>
		</rootHeight>
		<nodeHeights internalNodes="true">
			<parameter id="phased_RpL14.treeModel.internalNodeHeights"/>
		</nodeHeights>
		<nodeHeights internalNodes="true" rootNode="true">
			<parameter id="phased_RpL14.treeModel.allInternalNodeHeights"/>
		</nodeHeights>
</treeModel>
```

```
	<!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4, e88 )-->
	<discretizedBranchRates id="phased_1433.branchRates">
		<treeModel idref="phased_1433.treeModel"/>
		<distribution>
			<logNormalDistributionModel meanInRealSpace="true">
				<mean>
					<parameter id="phased_1433.ucld.mean" value="1.0" lower="0.0"/>
				</mean>
				<stdev>
					<parameter id="phased_1433.ucld.stdev" value="0.3333333333333333" lower="0.0"/>
				</stdev>
			</logNormalDistributionModel>
		</distribution>
		<rateCategories>
			<parameter id="phased_1433.branchRates.categories"/>
		</rateCategories>
	</discretizedBranchRates>
	<rateStatistic id="phased_1433.meanRate" name="phased_1433.meanRate" mode="mean" internal="true" external="true">
		<treeModel idref="phased_1433.treeModel"/>
		<discretizedBranchRates idref="phased_1433.branchRates"/>
	</rateStatistic>
	<rateStatistic id="phased_1433.coefficientOfVariation" name="phased_1433.coefficientOfVariation" mode="coefficientOfVariation" internal="true" external="true">
		<treeModel idref="phased_1433.treeModel"/>
		<discretizedBranchRates idref="phased_1433.branchRates"/>
	</rateStatistic>
	<rateCovarianceStatistic id="phased_1433.covariance" name="phased_1433.covariance">
		<treeModel idref="phased_1433.treeModel"/>
		<discretizedBranchRates idref="phased_1433.branchRates"/>
	</rateCovarianceStatistic>

	<!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4, e88 )-->
	<discretizedBranchRates id="aligned_COI.branchRates">
		<treeModel idref="aligned_COI.treeModel"/>
		<distribution>
			<logNormalDistributionModel meanInRealSpace="true">
				<mean>
					<parameter id="aligned_COI.ucld.mean" value="0.023" lower="0.0"/>
				</mean>
				<stdev>
					<parameter id="aligned_COI.ucld.stdev" value="0.3333333333333333" lower="0.0"/>
				</stdev>
			</logNormalDistributionModel>
		</distribution>
		<rateCategories>
			<parameter id="aligned_COI.branchRates.categories"/>
		</rateCategories>
	</discretizedBranchRates>
	<rateStatistic id="aligned_COI.meanRate" name="aligned_COI.meanRate" mode="mean" internal="true" external="true">
		<treeModel idref="aligned_COI.treeModel"/>
		<discretizedBranchRates idref="aligned_COI.branchRates"/>
	</rateStatistic>
```

```
        <rateStatistic id="aligned_COI.coefficientOfVariation" name="aligned_COI.coefficientOfVariation"
mode="coefficientOfVariation" internal="true" external="true">
                <treeModel idref="aligned_COI.treeModel"/>
                <discretizedBranchRates idref="aligned_COI.branchRates"/>
        </rateStatistic>
        <rateCovarianceStatistic id="aligned_COI.covariance" name="aligned_COI.covariance">
                <treeModel idref="aligned_COI.treeModel"/>
                <discretizedBranchRates idref="aligned_COI.branchRates"/>
        </rateCovarianceStatistic>

        <!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4,
e88 )-->
        <discretizedBranchRates id="aligned_COII.branchRates">
                <treeModel idref="aligned_COII.treeModel"/>
                <distribution>
                        <logNormalDistributionModel meanInRealSpace="true">
                                <mean>
                                        <parameter id="aligned_COII.ucld.mean" value="0.023"
lower="0.0"/>
                                </mean>
                                <stdev>
                                        <parameter id="aligned_COII.ucld.stdev"
value="0.3333333333333333" lower="0.0"/>
                                </stdev>
                        </logNormalDistributionModel>
                </distribution>
                <rateCategories>
                        <parameter id="aligned_COII.branchRates.categories"/>
                </rateCategories>
        </discretizedBranchRates>
        <rateStatistic id="aligned_COII.meanRate" name="aligned_COII.meanRate" mode="mean"
internal="true" external="true">
                <treeModel idref="aligned_COII.treeModel"/>
                <discretizedBranchRates idref="aligned_COII.branchRates"/>
        </rateStatistic>
        <rateStatistic id="aligned_COII.coefficientOfVariation" name="aligned_COII.coefficientOfVariation"
mode="coefficientOfVariation" internal="true" external="true">
                <treeModel idref="aligned_COII.treeModel"/>
                <discretizedBranchRates idref="aligned_COII.branchRates"/>
        </rateStatistic>
        <rateCovarianceStatistic id="aligned_COII.covariance" name="aligned_COII.covariance">
                <treeModel idref="aligned_COII.treeModel"/>
                <discretizedBranchRates idref="aligned_COII.branchRates"/>
        </rateCovarianceStatistic>

        <!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4,
e88 )-->
        <discretizedBranchRates id="phased_DNAJ.branchRates">
                <treeModel idref="phased_DNAJ.treeModel"/>
                <distribution>
                        <logNormalDistributionModel meanInRealSpace="true">
                                <mean>
                                        <parameter id="phased_DNAJ.ucld.mean" value="1.0"
lower="0.0"/>
                                </mean>
                                <stdev>
                                        <parameter id="phased_DNAJ.ucld.stdev"
value="0.3333333333333333" lower="0.0"/>
                                </stdev>
                        </logNormalDistributionModel>
                </distribution>
```

```
                <rateCategories>
                        <parameter id="phased_DNAJ.branchRates.categories"/>
                </rateCategories>
        </discretizedBranchRates>
        <rateStatistic id="phased_DNAJ.meanRate" name="phased_DNAJ.meanRate" mode="mean"
internal="true" external="true">
                <treeModel idref="phased_DNAJ.treeModel"/>
                <discretizedBranchRates idref="phased_DNAJ.branchRates"/>
        </rateStatistic>
        <rateStatistic id="phased_DNAJ.coefficientOfVariation" name="phased_DNAJ.coefficientOfVariation"
mode="coefficientOfVariation" internal="true" external="true">
                <treeModel idref="phased_DNAJ.treeModel"/>
                <discretizedBranchRates idref="phased_DNAJ.branchRates"/>
        </rateStatistic>
        <rateCovarianceStatistic id="phased_DNAJ.covariance" name="phased_DNAJ.covariance">
                <treeModel idref="phased_DNAJ.treeModel"/>
                <discretizedBranchRates idref="phased_DNAJ.branchRates"/>
        </rateCovarianceStatistic>

        <!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4,
e88 )-->
        <discretizedBranchRates id="Its2.branchRates">
                <treeModel idref="Its2.treeModel"/>
                <distribution>
                        <logNormalDistributionModel meanInRealSpace="true">
                                <mean>
                                        <parameter id="Its2.ucld.mean" value="1.0" lower="0.0"/>
                                </mean>
                                <stdev>
                                        <parameter id="Its2.ucld.stdev"
value="0.3333333333333333" lower="0.0"/>
                                </stdev>
                        </logNormalDistributionModel>
                </distribution>
                <rateCategories>
                        <parameter id="Its2.branchRates.categories"/>
                </rateCategories>
        </discretizedBranchRates>
        <rateStatistic id="Its2.meanRate" name="Its2.meanRate" mode="mean" internal="true"
external="true">
                <treeModel idref="Its2.treeModel"/>
                <discretizedBranchRates idref="Its2.branchRates"/>
        </rateStatistic>
        <rateStatistic id="Its2.coefficientOfVariation" name="Its2.coefficientOfVariation"
mode="coefficientOfVariation" internal="true" external="true">
                <treeModel idref="Its2.treeModel"/>
                <discretizedBranchRates idref="Its2.branchRates"/>
        </rateStatistic>
        <rateCovarianceStatistic id="Its2.covariance" name="Its2.covariance">
                <treeModel idref="Its2.treeModel"/>
                <discretizedBranchRates idref="Its2.branchRates"/>
        </rateCovarianceStatistic>

        <!-- The uncorrelated relaxed clock (Drummond, Ho, Phillips & Rambaut (2006) PLoS Biology 4,
e88 )-->
        <discretizedBranchRates id="phased_RpL14.branchRates">
                <treeModel idref="phased_RpL14.treeModel"/>
                <distribution>
                        <logNormalDistributionModel meanInRealSpace="true">
                                <mean>
                                        <parameter id="phased_RpL14.ucld.mean" value="1.0"
```

```
lower="0.0"/>
                                        </mean>
                                        <stdev>
                                                <parameter id="phased_RpL14.ucld.stdev"
value="0.3333333333333333" lower="0.0"/>
                                        </stdev>
                                </logNormalDistributionModel>
                        </distribution>
                        <rateCategories>
                                <parameter id="phased_RpL14.branchRates.categories"/>
                        </rateCategories>
                </discretizedBranchRates>
                <rateStatistic id="phased_RpL14.meanRate" name="phased_RpL14.meanRate" mode="mean"
internal="true" external="true">
                        <treeModel idref="phased_RpL14.treeModel"/>
                        <discretizedBranchRates idref="phased_RpL14.branchRates"/>
                </rateStatistic>
                <rateStatistic id="phased_RpL14.coefficientOfVariation"
name="phased_RpL14.coefficientOfVariation" mode="coefficientOfVariation" internal="true" external="true">
                        <treeModel idref="phased_RpL14.treeModel"/>
                        <discretizedBranchRates idref="phased_RpL14.branchRates"/>
                </rateStatistic>
                <rateCovarianceStatistic id="phased_RpL14.covariance" name="phased_RpL14.covariance">
                        <treeModel idref="phased_RpL14.treeModel"/>
                        <discretizedBranchRates idref="phased_RpL14.branchRates"/>
                </rateCovarianceStatistic>

                <!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)          -->
                <HKYModel id="phased_1433.hky">
                        <frequencies>
                                <frequencyModel dataType="nucleotide">
                                        <frequencies>
                                                <parameter id="phased_1433.frequencies" value="0.25
0.25 0.25 0.25"/>
                                        </frequencies>
                                </frequencyModel>
                        </frequencies>
                        <kappa>
                                <parameter id="phased_1433.kappa" value="2.0" lower="0.0"/>
                        </kappa>
                </HKYModel>

                <!-- site model                                                          -->
                <siteModel id="phased_1433.siteModel">
                        <substitutionModel>
                                <HKYModel idref="phased_1433.hky"/>
                        </substitutionModel>
                        <gammaShape gammaCategories="4">
                                <parameter id="phased_1433.alpha" value="0.5" lower="0.0"/>
                        </gammaShape>
                </siteModel>

                <!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)          -->
                <HKYModel id="aligned_COI.hky">
                        <frequencies>
                                <frequencyModel dataType="nucleotide">
                                        <frequencies>
                                                <parameter id="aligned_COI.frequencies" value="0.25
0.25 0.25 0.25"/>
                                        </frequencies>
                                </frequencyModel>
```

```
                </frequencies>
                <kappa>
                        <parameter id="aligned_COI.kappa" value="2.0" lower="0.0"/>
                </kappa>
        </HKYModel>

        <!-- site model                                                          -->
        <siteModel id="aligned_COI.siteModel">
                <substitutionModel>
                        <HKYModel idref="aligned_COI.hky"/>
                </substitutionModel>
                <gammaShape gammaCategories="4">
                        <parameter id="aligned_COI.alpha" value="0.5" lower="0.0"/>
                </gammaShape>
        </siteModel>

        <!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)        -->
        <HKYModel id="aligned_COII.hky">
                <frequencies>
                        <frequencyModel dataType="nucleotide">
                                <frequencies>
                                        <parameter   id="aligned_COII.frequencies"   value="0.25
0.25 0.25 0.25"/>
                                </frequencies>
                        </frequencyModel>
                </frequencies>
                <kappa>
                        <parameter id="aligned_COII.kappa" value="2.0" lower="0.0"/>
                </kappa>
        </HKYModel>

        <!-- site model                                                          -->
        <siteModel id="aligned_COII.siteModel">
                <substitutionModel>
                        <HKYModel idref="aligned_COII.hky"/>
                </substitutionModel>
                <gammaShape gammaCategories="4">
                        <parameter id="aligned_COII.alpha" value="0.5" lower="0.0"/>
                </gammaShape>
        </siteModel>

        <!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)        -->
        <HKYModel id="phased_DNAJ.hky">
                <frequencies>
                        <frequencyModel dataType="nucleotide">
                                <frequencies>
                                        <parameter   id="phased_DNAJ.frequencies"   value="0.25
0.25 0.25 0.25"/>
                                </frequencies>
                        </frequencyModel>
                </frequencies>
                <kappa>
                        <parameter id="phased_DNAJ.kappa" value="2.0" lower="0.0"/>
                </kappa>
        </HKYModel>

        <!-- site model                                                          -->
        <siteModel id="phased_DNAJ.siteModel">
                <substitutionModel>
                        <HKYModel idref="phased_DNAJ.hky"/>
                </substitutionModel>
```

```
		<gammaShape gammaCategories="4">
			<parameter id="phased_DNAJ.alpha" value="0.5" lower="0.0"/>
		</gammaShape>
	</siteModel>

	<!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)		-->
	<HKYModel id="Its2.hky">
		<frequencies>
			<frequencyModel dataType="nucleotide">
				<frequencies>
					<parameter id="Its2.frequencies" value="0.25 0.25 0.25
0.25"/>
				</frequencies>
			</frequencyModel>
		</frequencies>
		<kappa>
			<parameter id="Its2.kappa" value="2.0" lower="0.0"/>
		</kappa>
	</HKYModel>

	<!-- site model 		-->
	<siteModel id="Its2.siteModel">
		<substitutionModel>
			<HKYModel idref="Its2.hky"/>
		</substitutionModel>
		<gammaShape gammaCategories="4">
			<parameter id="Its2.alpha" value="0.5" lower="0.0"/>
		</gammaShape>
	</siteModel>

	<!-- The HKY substitution model (Hasegawa, Kishino & Yano, 1985)		-->
	<HKYModel id="phased_RpL14.hky">
		<frequencies>
			<frequencyModel dataType="nucleotide">
				<frequencies>
					<parameter id="phased_RpL14.frequencies" value="0.25
0.25 0.25 0.25"/>
				</frequencies>
			</frequencyModel>
		</frequencies>
		<kappa>
			<parameter id="phased_RpL14.kappa" value="2.0" lower="0.0"/>
		</kappa>
	</HKYModel>

	<!-- site model 		-->
	<siteModel id="phased_RpL14.siteModel">
		<substitutionModel>
			<HKYModel idref="phased_RpL14.hky"/>
		</substitutionModel>
		<gammaShape gammaCategories="4">
			<parameter id="phased_RpL14.alpha" value="0.5" lower="0.0"/>
		</gammaShape>
	</siteModel>

	<!-- Likelihood for tree given sequence data 		-->
	<treeLikelihood id="phased_1433.treeLikelihood" useAmbiguities="false">
		<patterns idref="phased_1433.patterns"/>
		<treeModel idref="phased_1433.treeModel"/>
		<siteModel idref="phased_1433.siteModel"/>
		<discretizedBranchRates idref="phased_1433.branchRates"/>
```

```
</treeLikelihood>

<!-- Likelihood for tree given sequence data                                    -->
<treeLikelihood id="aligned_COI.treeLikelihood" useAmbiguities="false">
        <patterns idref="aligned_COI.patterns"/>
        <treeModel idref="aligned_COI.treeModel"/>
        <siteModel idref="aligned_COI.siteModel"/>
        <discretizedBranchRates idref="aligned_COI.branchRates"/>
</treeLikelihood>

<!-- Likelihood for tree given sequence data                                    -->
<treeLikelihood id="aligned_COII.treeLikelihood" useAmbiguities="false">
        <patterns idref="aligned_COII.patterns"/>
        <treeModel idref="aligned_COII.treeModel"/>
        <siteModel idref="aligned_COII.siteModel"/>
        <discretizedBranchRates idref="aligned_COII.branchRates"/>
</treeLikelihood>

<!-- Likelihood for tree given sequence data                                    -->
<treeLikelihood id="phased_DNAJ.treeLikelihood" useAmbiguities="false">
        <patterns idref="phased_DNAJ.patterns"/>
        <treeModel idref="phased_DNAJ.treeModel"/>
        <siteModel idref="phased_DNAJ.siteModel"/>
        <discretizedBranchRates idref="phased_DNAJ.branchRates"/>
</treeLikelihood>

<!-- Likelihood for tree given sequence data                                    -->
<treeLikelihood id="Its2.treeLikelihood" useAmbiguities="false">
        <patterns idref="Its2.patterns"/>
        <treeModel idref="Its2.treeModel"/>
        <siteModel idref="Its2.siteModel"/>
        <discretizedBranchRates idref="Its2.branchRates"/>
</treeLikelihood>

<!-- Likelihood for tree given sequence data                                    -->
<treeLikelihood id="phased_RpL14.treeLikelihood" useAmbiguities="false">
        <patterns idref="phased_RpL14.patterns"/>
        <treeModel idref="phased_RpL14.treeModel"/>
        <siteModel idref="phased_RpL14.siteModel"/>
        <discretizedBranchRates idref="phased_RpL14.branchRates"/>
</treeLikelihood>

<!-- Species definition: binds taxa, species and gene trees                     -->
<species id="species">
        <sp id="An. belenrae">
                <taxon idref="B_S7-07-1"/>
                <taxon idref="B_S7-010-1"/>
                <taxon idref="B_S7-010-2"/>
                <taxon idref="B_M3-242-1"/>
                <taxon idref="B_M3-242-2"/>
                <taxon idref="B_S7-07"/>
                <taxon idref="B_S7-07_2"/>
                <taxon idref="B_S7-10"/>
                <taxon idref="B_M3-242"/>
                <taxon idref="B_S7-07_-1"/>
                <taxon idref="B_S7-07_-2"/>
                <taxon idref="B_S7-010_-1"/>
                <taxon idref="B_S7-010_-2"/>
                <taxon idref="B_S7-07-2"/>
                <taxon idref="B_S7-10-1"/>
                <taxon idref="B_S7-10-2"/>
```

```
</sp>
<sp id="An. gambiae">
        <taxon idref="G_XM_564587.3"/>
        <taxon idref="An._gambiae_DQ792578.1"/>
        <taxon idref="An._gambiae_DQ792577.1"/>
        <taxon idref="An._gambae_L20934.1_1"/>
        <taxon idref="An._gambae_L20934.1_2"/>
        <taxon idref="G_"/>
        <taxon idref="G_EU1046_1"/>
        <taxon idref="G_EU1046_2"/>
</sp>
<sp id="An. kleini">
        <taxon idref="K_PC020-1"/>
        <taxon idref="K_PC020-2"/>
        <taxon idref="K_YC024-1"/>
        <taxon idref="K_YC024-2"/>
        <taxon idref="K_YC080-1"/>
        <taxon idref="K_YC080-2"/>
        <taxon idref="K_YC024"/>
        <taxon idref="K_GQ265917.1"/>
        <taxon idref="K_PC020"/>
        <taxon idref="K_PC017"/>
        <taxon idref="K_YC080"/>
        <taxon idref="K_YC024_-1"/>
        <taxon idref="K_YC024_-2"/>
        <taxon idref="K_YC079-1"/>
        <taxon idref="K_YC079-2"/>
        <taxon idref="K_PC020_-1"/>
        <taxon idref="K_PC020_-2"/>
        <taxon idref="K_PC017-1"/>
        <taxon idref="K_PC017-2"/>
        <taxon idref="K_PC018-1"/>
        <taxon idref="K_PC018-2"/>
</sp>
<sp id="An. lesteri">
        <taxon idref="L_S7-18-1"/>
        <taxon idref="L_S7-18-2"/>
        <taxon idref="L_S7-24-1"/>
        <taxon idref="L_S7-24-2"/>
        <taxon idref="L_S7-30-1"/>
        <taxon idref="L_S7-30-2"/>
        <taxon idref="L_S7-31-1"/>
        <taxon idref="L_S7-31-2"/>
        <taxon idref="L_S7-24"/>
        <taxon idref="L_S7-30"/>
        <taxon idref="L_S7-31"/>
</sp>
<sp id="An. pullus">
        <taxon idref="P_YC052-1"/>
        <taxon idref="P_YC052-2"/>
        <taxon idref="P_YC068-1"/>
        <taxon idref="P_YC068-2"/>
        <taxon idref="P_YC070-1"/>
        <taxon idref="P_YC070-2"/>
        <taxon idref="P_YC075-1"/>
        <taxon idref="P_YC075-2"/>
        <taxon idref="P_YC048"/>
        <taxon idref="P_YC070"/>
        <taxon idref="P_YC075"/>
        <taxon idref="P_YC052"/>
        <taxon idref="P_YC068"/>
```

```
                <taxon idref="P_YC048-1"/>
                <taxon idref="P_YC048-2"/>
                <taxon idref="P_YC070_-1"/>
                <taxon idref="P_YC070_-2"/>
                <taxon idref="P_YC075_-1"/>
                <taxon idref="P_YC075_-2"/>
        </sp>
        <sp id="An. sinensis">
                <taxon idref="S_YC006-1"/>
                <taxon idref="S_YC006-2"/>
                <taxon idref="S_YC053-1"/>
                <taxon idref="S_YC053-2"/>
                <taxon idref="S_GR033-1"/>
                <taxon idref="S_GR033-2"/>
                <taxon idref="S_GR043-1"/>
                <taxon idref="S_GR043-2"/>
                <taxon idref="S_TL021-1"/>
                <taxon idref="S_TL021-2"/>
                <taxon idref="S_TL022-1"/>
                <taxon idref="S_TL022-2"/>
                <taxon idref="S_TL021"/>
                <taxon idref="S_TL022"/>
                <taxon idref="S_YC006"/>
                <taxon idref="S_YC053"/>
                <taxon idref="S_GR033"/>
                <taxon idref="S_GR043"/>
        </sp>
        <sp id="An. sineroides">
                <taxon idref="SR_YY026-1"/>
                <taxon idref="SR_YY026-2"/>
                <taxon idref="SR_YY026"/>
                <taxon idref="SR_YY026_2"/>
                <taxon idref="SR_YYC026"/>
                <taxon idref="SR_YYC026_2"/>
                <taxon idref="SR_DQ177505.1-1"/>
                <taxon idref="SR_DQ177505.1-2"/>
        </sp>

        <!-- Collection of Gene Trees                                                -->
        <geneTrees id="geneTrees">
                <gtree ploidy="2.0">
                        <treeModel idref="phased_1433.treeModel"/>
                </gtree>
                <gtree ploidy="0.5">
                        <treeModel idref="aligned_COI.treeModel"/>
                </gtree>
                <gtree ploidy="0.5">
                        <treeModel idref="aligned_COII.treeModel"/>
                </gtree>
                <gtree ploidy="2.0">
                        <treeModel idref="phased_DNAJ.treeModel"/>
                </gtree>
                <gtree ploidy="2.0">
                        <treeModel idref="Its2.treeModel"/>
                </gtree>
                <gtree ploidy="2.0">
                        <treeModel idref="phased_RpL14.treeModel"/>
                </gtree>
        </geneTrees>
</species>
```

```
<!-- full species set for species tree root height                    -->
<taxa id="allSpecies">
        <sp idref="An. belenrae"/>
        <sp idref="An. gambiae"/>
        <sp idref="An. kleini"/>
        <sp idref="An. lesteri"/>
        <sp idref="An. pullus"/>
        <sp idref="An. sinensis"/>
        <sp idref="An. sineroides"/>
</taxa>
<taxa id="ingroup">
        <taxon idref="An. belenrae"/>
        <taxon idref="An. kleini"/>
        <taxon idref="An. lesteri"/>
        <taxon idref="An. pullus"/>
        <taxon idref="An. sinensis"/>
        <taxon idref="An. sineroides"/>
</taxa>

<!-- species starting tree for calibration                            -->
<coalescentTree id="spStartingTree">
        <constrainedTaxa>
                <taxa idref="allSpecies"/>
                <tmrca monophyletic="true">
                        <taxa idref="ingroup"/>
                </tmrca>
        </constrainedTaxa>
        <constantSize id="spInitDemo" units="substitutions">
                <populationSize>
                        <parameter id="sp.popSize" value="0.084"/>
                </populationSize>
        </constantSize>
</coalescentTree>

<!-- Species Tree: Provides Per branch demographic function           -->
<speciesTree id="sptree" constantRoot="true">
        <species idref="species"/>
        <sppSplitPopulations value="0.084">
                <parameter id="speciesTree.splitPopSize"/>
        </sppSplitPopulations>
        <coalescentTree idref="spStartingTree"/>
</speciesTree>

<!-- Species Sets                                                     -->
<tmrcaStatistic id="tmrca(ingroup)">
        <mrca>
                <taxa idref="ingroup"/>
        </mrca>
        <speciesTree idref="sptree"/>
</tmrcaStatistic>
<monophylyStatistic id="monophyly(ingroup)">
        <mrca>
                <taxa idref="ingroup"/>
        </mrca>
        <speciesTree idref="sptree"/>
</monophylyStatistic>

<!-- Species tree prior: Yule Model                                   -->
<yuleModel id="yule" units="substitutions">
        <birthRate>
                <parameter id="species.yule.birthRate" value="1.0" lower="0.0"/>
```

```
                </birthRate>
        </yuleModel>

        <!-- Species Tree Likelihood: Yule Model                                    -->
        <speciationLikelihood id="speciation.likelihood">
                <model>
                        <yuleModel idref="yule"/>
                </model>
                <speciesTree>
                        <speciesTree idref="sptree"/>
                </speciesTree>
        </speciationLikelihood>

        <!-- Species Tree: tmrcaStatistic                                           -->
        <tmrcaStatistic id="speciesTree.rootHeight" name="speciesTree.rootHeight">
                <speciesTree idref="sptree"/>
                <mrca>
                        <taxa idref="allSpecies"/>
                </mrca>
        </tmrcaStatistic>

        <!-- Species Tree: Coalescent likelihood for gene trees under species tree  -->
        <speciesCoalescent id="species.coalescent">
                <species idref="species"/>
                <speciesTree idref="sptree"/>
        </speciesCoalescent>

        <!-- Species tree prior: gama2 + gamma4                                     -->
        <mixedDistributionLikelihood id="species.popSizesLikelihood">
                <distribution0>
                        <gammaDistributionModel>
                                <shape>
                                        2
                                </shape>
                                <scale>
                                        <parameter id="species.popMean" value="1.0"
lower="0.0"/>
                                </scale>
                        </gammaDistributionModel>
                </distribution0>
                <distribution1>
                        <gammaDistributionModel>
                                <shape>
                                        4
                                </shape>
                                <scale>
                                        <parameter idref="species.popMean"/>
                                </scale>
                        </gammaDistributionModel>
                </distribution1>
                <data>
                        <parameter idref="speciesTree.splitPopSize"/>
                </data>
                <indicators>
                        <parameter value="1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0"/>
                </indicators>
        </mixedDistributionLikelihood>

        <!-- Define operators                                                       -->
        <operators id="operators">
                <scaleOperator scaleFactor="0.75" weight="0.1">
```

```
            <parameter idref="phased_1433.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="phased_1433.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="phased_1433.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="aligned_COI.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="aligned_COI.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="aligned_COI.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="aligned_COII.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="aligned_COII.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="aligned_COII.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="phased_DNAJ.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="phased_DNAJ.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="phased_DNAJ.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="Its2.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="Its2.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="Its2.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="phased_RpL14.kappa"/>
</scaleOperator>
<deltaExchange delta="0.01" weight="0.1">
            <parameter idref="phased_RpL14.frequencies"/>
</deltaExchange>
<scaleOperator scaleFactor="0.75" weight="0.1">
            <parameter idref="phased_RpL14.alpha"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="3">
            <parameter idref="phased_1433.ucld.mean"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="3">
            <parameter idref="phased_1433.ucld.stdev"/>
</scaleOperator>
<scaleOperator scaleFactor="0.75" weight="3">
            <parameter idref="aligned_COI.ucld.mean"/>
```

```
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="aligned_COI.ucld.stdev"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="aligned_COII.ucld.mean"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="aligned_COII.ucld.stdev"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="phased_DNAJ.ucld.mean"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="phased_DNAJ.ucld.stdev"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="Its2.ucld.mean"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="Its2.ucld.stdev"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="phased_RpL14.ucld.mean"/>
                </scaleOperator>
                <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="phased_RpL14.ucld.stdev"/>
                </scaleOperator>
                <upDownOperator scaleFactor="0.75" weight="30">
                        <up>
                                <parameter idref="phased_1433.ucld.mean"/>
                                <parameter idref="aligned_COI.ucld.mean"/>
                                <parameter idref="aligned_COII.ucld.mean"/>
                                <parameter idref="phased_DNAJ.ucld.mean"/>
                                <parameter idref="Its2.ucld.mean"/>
                                <parameter idref="phased_RpL14.ucld.mean"/>
                                <parameter idref="species.yule.birthRate"/>
                        </up>
                        <down>
                                <speciesTree idref="sptree"/>
                                <parameter idref="species.popMean"/>
                                <parameter idref="speciesTree.splitPopSize"/>
                                <parameter idref="phased_1433.treeModel.allInternalNodeHeights"/>
                                <parameter idref="aligned_COI.treeModel.allInternalNodeHeights"/>
                                <parameter idref="aligned_COII.treeModel.allInternalNodeHeights"/>
                                <parameter
idref="phased_DNAJ.treeModel.allInternalNodeHeights"/>
                                <parameter idref="Its2.treeModel.allInternalNodeHeights"/>
                                <parameter
idref="phased_RpL14.treeModel.allInternalNodeHeights"/>
                        </down>
                </upDownOperator>
                <subtreeSlide size="0.006900000000000001" gaussian="true" weight="15">
                        <treeModel idref="phased_1433.treeModel"/>
                </subtreeSlide>
                <narrowExchange weight="15">
                        <treeModel idref="phased_1433.treeModel"/>
                </narrowExchange>
                <wideExchange weight="3">
                        <treeModel idref="phased_1433.treeModel"/>
                </wideExchange>
```

```
<wilsonBalding weight="3">
        <treeModel idref="phased_1433.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
        <parameter idref="phased_1433.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
        <parameter idref="phased_1433.treeModel.internalNodeHeights"/>
</uniformOperator>
<subtreeSlide size="0.2" gaussian="true" weight="15">
        <treeModel idref="aligned_COI.treeModel"/>
</subtreeSlide>
<narrowExchange weight="15">
        <treeModel idref="aligned_COI.treeModel"/>
</narrowExchange>
<wideExchange weight="3">
        <treeModel idref="aligned_COI.treeModel"/>
</wideExchange>
<wilsonBalding weight="3">
        <treeModel idref="aligned_COI.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
        <parameter idref="aligned_COI.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
        <parameter idref="aligned_COI.treeModel.internalNodeHeights"/>
</uniformOperator>
<subtreeSlide size="0.18" gaussian="true" weight="15">
        <treeModel idref="aligned_COII.treeModel"/>
</subtreeSlide>
<narrowExchange weight="15">
        <treeModel idref="aligned_COII.treeModel"/>
</narrowExchange>
<wideExchange weight="3">
        <treeModel idref="aligned_COII.treeModel"/>
</wideExchange>
<wilsonBalding weight="3">
        <treeModel idref="aligned_COII.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
        <parameter idref="aligned_COII.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
        <parameter idref="aligned_COII.treeModel.internalNodeHeights"/>
</uniformOperator>
<subtreeSlide size="0.0048000000000000004" gaussian="true" weight="15">
        <treeModel idref="phased_DNAJ.treeModel"/>
</subtreeSlide>
<narrowExchange weight="15">
        <treeModel idref="phased_DNAJ.treeModel"/>
</narrowExchange>
<wideExchange weight="3">
        <treeModel idref="phased_DNAJ.treeModel"/>
</wideExchange>
<wilsonBalding weight="3">
        <treeModel idref="phased_DNAJ.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
        <parameter idref="phased_DNAJ.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
```

```
            <parameter idref="phased_DNAJ.treeModel.internalNodeHeights"/>
</uniformOperator>
<subtreeSlide size="0.02" gaussian="true" weight="15">
            <treeModel idref="Its2.treeModel"/>
</subtreeSlide>
<narrowExchange weight="15">
            <treeModel idref="Its2.treeModel"/>
</narrowExchange>
<wideExchange weight="3">
            <treeModel idref="Its2.treeModel"/>
</wideExchange>
<wilsonBalding weight="3">
            <treeModel idref="Its2.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
            <parameter idref="Its2.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
            <parameter idref="Its2.treeModel.internalNodeHeights"/>
</uniformOperator>
<subtreeSlide size="0.0090" gaussian="true" weight="15">
            <treeModel idref="phased_RpL14.treeModel"/>
</subtreeSlide>
<narrowExchange weight="15">
            <treeModel idref="phased_RpL14.treeModel"/>
</narrowExchange>
<wideExchange weight="3">
            <treeModel idref="phased_RpL14.treeModel"/>
</wideExchange>
<wilsonBalding weight="3">
            <treeModel idref="phased_RpL14.treeModel"/>
</wilsonBalding>
<scaleOperator scaleFactor="0.75" weight="3">
            <parameter idref="phased_RpL14.treeModel.rootHeight"/>
</scaleOperator>
<uniformOperator weight="30">
            <parameter idref="phased_RpL14.treeModel.internalNodeHeights"/>
</uniformOperator>
<upDownOperator scaleFactor="0.75" weight="3">
            <up>
                        <parameter idref="phased_1433.ucld.mean"/>
            </up>
            <down>
                        <parameter idref="phased_1433.treeModel.allInternalNodeHeights"/>
            </down>
</upDownOperator>
<swapOperator size="1" weight="10" autoOptimize="false">
            <parameter idref="phased_1433.branchRates.categories"/>
</swapOperator>
<uniformIntegerOperator weight="10">
            <parameter idref="phased_1433.branchRates.categories"/>
</uniformIntegerOperator>
<upDownOperator scaleFactor="0.75" weight="3">
            <up>
                        <parameter idref="aligned_COI.ucld.mean"/>
            </up>
            <down>
                        <parameter idref="aligned_COI.treeModel.allInternalNodeHeights"/>
            </down>
</upDownOperator>
<swapOperator size="1" weight="10" autoOptimize="false">
```

```
                        <parameter idref="aligned_COI.branchRates.categories"/>
                    </swapOperator>
                    <uniformIntegerOperator weight="10">
                        <parameter idref="aligned_COI.branchRates.categories"/>
                    </uniformIntegerOperator>
                    <upDownOperator scaleFactor="0.75" weight="3">
                        <up>
                            <parameter idref="aligned_COII.ucld.mean"/>
                        </up>
                        <down>
                            <parameter idref="aligned_COII.treeModel.allInternalNodeHeights"/>
                        </down>
                    </upDownOperator>
                    <swapOperator size="1" weight="10" autoOptimize="false">
                        <parameter idref="aligned_COII.branchRates.categories"/>
                    </swapOperator>
                    <uniformIntegerOperator weight="10">
                        <parameter idref="aligned_COII.branchRates.categories"/>
                    </uniformIntegerOperator>
                    <upDownOperator scaleFactor="0.75" weight="3">
                        <up>
                            <parameter idref="phased_DNAJ.ucld.mean"/>
                        </up>
                        <down>
                            <parameter
idref="phased_DNAJ.treeModel.allInternalNodeHeights"/>
                        </down>
                    </upDownOperator>
                    <swapOperator size="1" weight="10" autoOptimize="false">
                        <parameter idref="phased_DNAJ.branchRates.categories"/>
                    </swapOperator>
                    <uniformIntegerOperator weight="10">
                        <parameter idref="phased_DNAJ.branchRates.categories"/>
                    </uniformIntegerOperator>
                    <upDownOperator scaleFactor="0.75" weight="3">
                        <up>
                            <parameter idref="Its2.ucld.mean"/>
                        </up>
                        <down>
                            <parameter idref="Its2.treeModel.allInternalNodeHeights"/>
                        </down>
                    </upDownOperator>
                    <swapOperator size="1" weight="10" autoOptimize="false">
                        <parameter idref="Its2.branchRates.categories"/>
                    </swapOperator>
                    <uniformIntegerOperator weight="10">
                        <parameter idref="Its2.branchRates.categories"/>
                    </uniformIntegerOperator>
                    <upDownOperator scaleFactor="0.75" weight="3">
                        <up>
                            <parameter idref="phased_RpL14.ucld.mean"/>
                        </up>
                        <down>
                            <parameter
idref="phased_RpL14.treeModel.allInternalNodeHeights"/>
                        </down>
                    </upDownOperator>
                    <swapOperator size="1" weight="10" autoOptimize="false">
                        <parameter idref="phased_RpL14.branchRates.categories"/>
                    </swapOperator>
                    <uniformIntegerOperator weight="10">
```

```
                        <parameter idref="phased_RpL14.branchRates.categories"/>
                    </uniformIntegerOperator>
                    <scaleOperator scaleFactor="0.9" weight="5">
                        <parameter idref="species.popMean"/>
                    </scaleOperator>
                    <scaleOperator scaleFactor="0.75" weight="3">
                        <parameter idref="species.yule.birthRate"/>
                    </scaleOperator>
                    <scaleOperator scaleFactor="0.5" weight="94">
                        <parameter idref="speciesTree.splitPopSize"/>
                    </scaleOperator>
                    <nodeReHeight weight="94">
                        <species idref="species"/>
                        <speciesTree idref="sptree"/>
                    </nodeReHeight>
                </operators>

                <!-- Define MCMC                                                    -->
                <mcmc id="mcmc" chainLength="10000000" autoOptimize="true" operatorAnalysis="ALL.ops.txt">
                    <posterior id="posterior">
                        <prior id="prior">
                            <speciesCoalescent idref="species.coalescent"/>
                            <mixedDistributionLikelihood idref="species.popSizesLikelihood"/>
                            <speciationLikelihood idref="speciation.likelihood"/>
                            <booleanLikelihood>
                                <monophylyStatistic idref="monophyly(ingroup)"/>
                            </booleanLikelihood>
                            <logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
                                <parameter idref="phased_1433.kappa"/>
                            </logNormalPrior>
                            <uniformPrior lower="0.0" upper="1.0">
                                <parameter idref="phased_1433.frequencies"/>
                            </uniformPrior>
                            <exponentialPrior mean="0.5" offset="0.0">
                                <parameter idref="phased_1433.alpha"/>
                            </exponentialPrior>
                            <logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
                                <parameter idref="aligned_COI.kappa"/>
                            </logNormalPrior>
                            <uniformPrior lower="0.0" upper="1.0">
                                <parameter idref="aligned_COI.frequencies"/>
                            </uniformPrior>
                            <exponentialPrior mean="0.5" offset="0.0">
                                <parameter idref="aligned_COI.alpha"/>
                            </exponentialPrior>
                            <logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
                                <parameter idref="aligned_COII.kappa"/>
                            </logNormalPrior>
                            <uniformPrior lower="0.0" upper="1.0">
                                <parameter idref="aligned_COII.frequencies"/>
                            </uniformPrior>
                            <exponentialPrior mean="0.5" offset="0.0">
                                <parameter idref="aligned_COII.alpha"/>
                            </exponentialPrior>
                            <logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
                                <parameter idref="phased_DNAJ.kappa"/>
                            </logNormalPrior>
```

<uniformPrior lower="0.0" upper="1.0">
<parameter idref="phased_DNAJ.frequencies"/>
</uniformPrior>
<exponentialPrior mean="0.5" offset="0.0">
<parameter idref="phased_DNAJ.alpha"/>
</exponentialPrior>
<logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
<parameter idref="Its2.kappa"/>
</logNormalPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="Its2.frequencies"/>
</uniformPrior>
<exponentialPrior mean="0.5" offset="0.0">
<parameter idref="Its2.alpha"/>
</exponentialPrior>
<logNormalPrior mean="1.0" stdev="1.25" offset="0.0"
meanInRealSpace="false">
<parameter idref="phased_RpL14.kappa"/>
</logNormalPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="phased_RpL14.frequencies"/>
</uniformPrior>
<exponentialPrior mean="0.5" offset="0.0">
<parameter idref="phased_RpL14.alpha"/>
</exponentialPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="phased_1433.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0E100">
<parameter idref="phased_1433.ucld.mean"/>
</uniformPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="aligned_COI.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="aligned_COI.ucld.mean"/>
</uniformPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="aligned_COII.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="aligned_COII.ucld.mean"/>
</uniformPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="phased_DNAJ.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="phased_DNAJ.ucld.mean"/>
</uniformPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="Its2.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="Its2.ucld.mean"/>
</uniformPrior>
<exponentialPrior mean="0.3333333333333333" offset="0.0">
<parameter idref="phased_RpL14.ucld.stdev"/>
</exponentialPrior>
<uniformPrior lower="0.0" upper="1.0">
<parameter idref="phased_RpL14.ucld.mean"/>

```
                        </uniformPrior>
                        <oneOnXPrior>
                                <parameter idref="species.popMean"/>
                        </oneOnXPrior>
                        <oneOnXPrior>
                                <parameter idref="species.yule.birthRate"/>
                        </oneOnXPrior>
                </prior>
                <likelihood id="likelihood">
                        <treeLikelihood idref="phased_1433.treeLikelihood"/>
                        <treeLikelihood idref="aligned_COI.treeLikelihood"/>
                        <treeLikelihood idref="aligned_COII.treeLikelihood"/>
                        <treeLikelihood idref="phased_DNAJ.treeLikelihood"/>
                        <treeLikelihood idref="Its2.treeLikelihood"/>
                        <treeLikelihood idref="phased_RpL14.treeLikelihood"/>
                </likelihood>
</posterior>
<operators idref="operators"/>

<!-- write log to screen                                                    -->
<log id="screenLog" logEvery="1000">
                <column label="Posterior" dp="4" width="12">
                        <posterior idref="posterior"/>
                </column>
                <column label="Prior" dp="4" width="12">
                        <prior idref="prior"/>
                </column>
                <column label="Likelihood" dp="4" width="12">
                        <likelihood idref="likelihood"/>
                </column>
                <column label="PopMean" dp="4" width="12">
                        <parameter idref="species.popMean"/>
                </column>
                <column label="phased_1433.rootHeight" sf="6" width="12">
                        <parameter idref="phased_1433.treeModel.rootHeight"/>
                </column>
                <column label="aligned_COI.rootHeight" sf="6" width="12">
                        <parameter idref="aligned_COI.treeModel.rootHeight"/>
                </column>
                <column label="aligned_COII.rootHeight" sf="6" width="12">
                        <parameter idref="aligned_COII.treeModel.rootHeight"/>
                </column>
                <column label="phased_DNAJ.rootHeight" sf="6" width="12">
                        <parameter idref="phased_DNAJ.treeModel.rootHeight"/>
                </column>
                <column label="Its2.rootHeight" sf="6" width="12">
                        <parameter idref="Its2.treeModel.rootHeight"/>
                </column>
                <column label="phased_RpL14.rootHeight" sf="6" width="12">
                        <parameter idref="phased_RpL14.treeModel.rootHeight"/>
                </column>
                <column label="phased_1433.ucld.mean" sf="6" width="12">
                        <parameter idref="phased_1433.ucld.mean"/>
                </column>
                <column label="aligned_COI.ucld.mean" sf="6" width="12">
                        <parameter idref="aligned_COI.ucld.mean"/>
                </column>
                <column label="aligned_COII.ucld.mean" sf="6" width="12">
                        <parameter idref="aligned_COII.ucld.mean"/>
                </column>
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            </column>
            <column label="Its2.ucld.mean" sf="6" width="12">
                <parameter idref="Its2.ucld.mean"/>
            </column>
            <column label="phased_RpL14.ucld.mean" sf="6" width="12">
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</log>

<!-- write log to file                                                    -->
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            <prior idref="prior"/>
            <likelihood idref="likelihood"/>
            <speciesCoalescent idref="species.coalescent"/>
            <mixedDistributionLikelihood idref="species.popSizesLikelihood"/>
            <speciationLikelihood idref="speciation.likelihood"/>
            <parameter idref="species.popMean"/>
            <parameter idref="speciesTree.splitPopSize"/>
            <parameter idref="species.yule.birthRate"/>
            <tmrcaStatistic idref="speciesTree.rootHeight"/>
            <parameter idref="phased_1433.treeModel.rootHeight"/>
            <parameter idref="aligned_COI.treeModel.rootHeight"/>
            <parameter idref="aligned_COII.treeModel.rootHeight"/>
            <parameter idref="phased_DNAJ.treeModel.rootHeight"/>
            <parameter idref="Its2.treeModel.rootHeight"/>
            <parameter idref="phased_RpL14.treeModel.rootHeight"/>
            <tmrcaStatistic idref="tmrca(ingroup)"/>
            <parameter idref="phased_1433.kappa"/>
            <parameter idref="phased_1433.frequencies"/>
            <parameter idref="phased_1433.alpha"/>
            <parameter idref="aligned_COI.kappa"/>
            <parameter idref="aligned_COI.frequencies"/>
            <parameter idref="aligned_COI.alpha"/>
            <parameter idref="aligned_COII.kappa"/>
            <parameter idref="aligned_COII.frequencies"/>
            <parameter idref="aligned_COII.alpha"/>
            <parameter idref="phased_DNAJ.kappa"/>
            <parameter idref="phased_DNAJ.frequencies"/>
            <parameter idref="phased_DNAJ.alpha"/>
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            <parameter idref="Its2.frequencies"/>
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            <parameter idref="phased_RpL14.frequencies"/>
            <parameter idref="phased_RpL14.alpha"/>
            <parameter idref="phased_1433.ucld.mean"/>
            <parameter idref="phased_1433.ucld.stdev"/>
            <parameter idref="aligned_COI.ucld.mean"/>
            <parameter idref="aligned_COI.ucld.stdev"/>
            <parameter idref="aligned_COII.ucld.mean"/>
            <parameter idref="aligned_COII.ucld.stdev"/>
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            <parameter idref="phased_DNAJ.ucld.stdev"/>
            <parameter idref="Its2.ucld.mean"/>
            <parameter idref="Its2.ucld.stdev"/>
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            <parameter idref="phased_RpL14.ucld.stdev"/>
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```

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                <rateStatistic idref="aligned_COII.meanRate"/>
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        <!-- write tree log to file                                                -->
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                <discretizedBranchRates idref="aligned_COII.branchRates"/>
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        </logTree>
        <logTree id="phased_DNAJ.treeFileLog" logEvery="1000" nexusFormat="true"
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</beast>
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Appendix 2. Input file for IM analysis

Ansinensis and Ankleini IM analysis based on seven locus
seven locus test
population1 population2
7
locus1 10 7 345 H 0.25 0.00000000023
pop1_YC01
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pop1_YC08
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pop1_YC09
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Appendix 3. Haplotype list of *Anopheles sinensis* s.s. mitochondrial DNA sequences

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Hap_22
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATATATAATTAATTAATTTATTATTAATTTTATTAATAGACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_23
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAACTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAGTTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_24
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTAAAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_25
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAATAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_26
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTTATTTATATATATTTTATTTTATAACT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTGATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_27
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTACAAT
TAATTTAATTTATATATAATTAATTAATTTATTATTAATTTTATTAATAGACAATAATTTTAAATTATTGTCTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_28
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTGATTTTATAATT
AATTTAAATTATATATAATTAATTAATTTATTATTAATTTTGTTAATAGACAATAATTTTAAATTATTGTCTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_29
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTGATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAGACAATAATTTTAAATTATTGTCTATT
ATATATAATATTTATATACGATGTATATATATATATATAAATTTATTATTAATTAATATAT

Hap_30
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTAATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_31
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTACTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_32
TAATTTTTTTTTTTTTTTTTTATTATAATTAATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAAC
TAATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTGATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_33
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTGATTTTATAATT
AATTTAATTTATGTAAAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_34
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAACT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_35
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTAAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_36

TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATACTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_37
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATCTAATTTTATAATT
AATTAAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATTTATAAATTTATTATTAATTAATATAT

Hap_38
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AACTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_39
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATGTATTTAATTTTATAATT
AATTTAACTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_40
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTTTT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_41
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTTTAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_42
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATGGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_43
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTTTAATTAATTAATTTATTATTAATTTTATTAATAAATAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_44
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATCTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAATAATAATTTTAAATTATTATTTATTA
TATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_45
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATAAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_46
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAATAATAATTTTAAATTATTGTTTATT
ATATATAAAATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_47
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAACTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_48
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTTATTTTATAATT

AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_49
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTACATATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTCTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_50
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAGTT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_51
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AAGTTAATTTATGTATAATTAATTAATTTATTATTGATTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_52
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATATATAATTAATTAATTTATTATTAATTTTATTAATAGACAATAATTTAAAATTATTGTCTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_53
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTGATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAACCAATAATTTTAAATTATTGTTTATT
ATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_54
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAATTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTGT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_55
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAACTTTATTAATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATGTATATATATATATAAATTTATTATTAATTAATATAT

Hap_56
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTGAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAACAATAATTTTAAATTATTGTTTGT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_57
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAACT
AATTTAATTTATGTTTAATTAATTAATTTATTATTAATTTTATTGATAAACAATAATTTTAAATTATTGTTTAT
TATATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Hap_58
TAATTTTTTTTTTTTTTTTTTATTATAATTTATTTAATTAAAGTTAATTAATTTATATATATTTAATTTTATAATT
AATTTAATTTATGTATAATTAATTAATTTATTATTAATTTTATTAATAAATAATAATTTTAAATTATTATTTATTA
TATATAATATTTATATACGATATATATATATATATAAATTTATTATTAATTAATATAT

Appendix 4. Input file for Arlequin of *Anopheles sinensis* s.s. mitochondrial DNA sequences

```
#     Project File generated by DnaSP Ver. 5.10.01;       24 - April - 2012
#     ================================================================

# Information from file 315_21grouped.nex
# Number of sequences: 315      Number of sequences used: 315
# Number of Sites in the complete Data File: 210
# Selected Region:   1-210
# Sites with alignment gaps:   not considered
# Invariable sites:   included
# Number of Sites in "1.hap" file: 210


[Profile]
    Title = "Haplotype Data from 315_21grouped.nex DnaSP file"
    NbSamples = 21
    DataType = DNA
    GenotypicData = 0
    LocusSeparator = NONE
    MissingData = "?"
    CompDistMatrix = 1


[Data]

[[HaplotypeDefinition]]
    HaplList = EXTERN "1.hap"

[[Samples]]
    SampleName = "AD"
    SampleSize = 11
    SampleData= {
        Hap_1 1
        Hap_2 1
        Hap_3 2
        Hap_4 1
        Hap_5 1
        Hap_6 2
        Hap_7 1
        Hap_8 1
        Hap_9 1
}
    SampleName = "BY"
    SampleSize = 7
    SampleData= {
        Hap_2 4
        Hap_4 2
        Hap_7 1
}
    SampleName = "CC"
    SampleSize = 14
    SampleData= {
        Hap_2 8
        Hap_4 2
        Hap_7 1
```

```
        Hap_10 1
        Hap_11 1
        Hap_12 1
}
    SampleName = "CH"
    SampleSize = 13
    SampleData= {
        Hap_4 10
        Hap_6 1
        Hap_13 1
        Hap_14 1
}
    SampleName = "DY"
    SampleSize = 17
    SampleData= {
        Hap_2 5
        Hap_4 7
        Hap_6 1
        Hap_12 1
        Hap_15 1
        Hap_16 1
        Hap_17 1
}
    SampleName = "ER"
    SampleSize = 25
    SampleData= {
        Hap_4 3
        Hap_6 3
        Hap_7 2
        Hap_8 3
        Hap_12 1
        Hap_13 1
        Hap_15 2
        Hap_17 1
        Hap_18 1
        Hap_19 1
        Hap_20 1
        Hap_21 1
        Hap_22 1
        Hap_23 1
        Hap_24 1
        Hap_25 1
        Hap_26 1
}
    SampleName = "GP"
    SampleSize = 12
    SampleData= {
        Hap_2 6
        Hap_4 4
        Hap_8 1
        Hap_12 1
}
    SampleName = "GR"
    SampleSize = 19
    SampleData= {
        Hap_4 4
        Hap_5 1
        Hap_6 2
        Hap_7 2
        Hap_8 1
        Hap_12 2
```

```
        Hap_27 2
        Hap_28 1
        Hap_29 1
        Hap_30 1
        Hap_31 1
        Hap_32 1
}
    SampleName = "JA"
    SampleSize = 19
    SampleData= {
        Hap_2 7
        Hap_4 2
        Hap_6 1
        Hap_8 1
        Hap_15 1
        Hap_17 1
        Hap_22 4
        Hap_33 1
        Hap_34 1
}
    SampleName = "JI"
    SampleSize = 19
    SampleData= {
        Hap_4 2
        Hap_6 4
        Hap_7 1
        Hap_8 2
        Hap_9 1
        Hap_10 1
        Hap_12 3
        Hap_13 1
        Hap_35 1
        Hap_36 1
        Hap_37 1
        Hap_38 1
}
    SampleName = "JU"
    SampleSize = 9
    SampleData= {
        Hap_1 1
        Hap_2 4
        Hap_17 1
        Hap_39 1
        Hap_40 1
        Hap_41 1
}
    SampleName = "KP"
    SampleSize = 16
    SampleData= {
        Hap_2 7
        Hap_4 3
        Hap_6 1
        Hap_7 1
        Hap_12 2
        Hap_42 1
        Hap_43 1
}
    SampleName = "NA"
    SampleSize = 16
    SampleData= {
        Hap_4 3
```

```
        Hap_6 1
        Hap_7 1
        Hap_12 1
        Hap_15 3
        Hap_17 1
        Hap_44 1
        Hap_45 1
        Hap_46 1
        Hap_47 1
        Hap_48 1
        Hap_49 1
}
    SampleName = "PJ"
    SampleSize = 26
    SampleData= {
        Hap_1 1
        Hap_2 9
        Hap_4 8
        Hap_6 1
        Hap_7 2
        Hap_8 1
        Hap_12 1
        Hap_50 1
        Hap_51 1
        Hap_52 1
}
    SampleName = "SR"
    SampleSize = 19
    SampleData= {
        Hap_2 8
        Hap_4 4
        Hap_6 3
        Hap_12 2
        Hap_53 1
        Hap_54 1
}
    SampleName = "TA"
    SampleSize = 13
    SampleData= {
        Hap_2 8
        Hap_4 3
        Hap_6 1
        Hap_7 1
}
    SampleName = "TW"
    SampleSize = 20
    SampleData= {
        Hap_4 14
        Hap_6 1
        Hap_15 3
        Hap_55 1
        Hap_56 1
}
    SampleName = "UJ"
    SampleSize = 10
    SampleData= {
        Hap_3 1
        Hap_4 4
        Hap_6 1
        Hap_7 1
        Hap_12 1
```

```
        Hap_14 1
        Hap_17 1
}
    SampleName = "YC"
    SampleSize = 10
    SampleData= {
        Hap_2 4
        Hap_4 2
        Hap_6 2
        Hap_7 1
        Hap_12 1
}
    SampleName = "YJ"
    SampleSize = 12
    SampleData= {
        Hap_2 4
        Hap_4 3
        Hap_6 2
        Hap_12 1
        Hap_57 1
        Hap_58 1
}
    SampleName = "YY"
    SampleSize = 8
    SampleData= {
        Hap_2 3
        Hap_4 2
        Hap_6 1
        Hap_7 1
        Hap_50 1
}


            [[Structure]]

                    StructureName="New Edited Structure"
                    NbGroups=3

                    Group={
                            "AD"
                            "ER"
                            "GR"
                            "JI"
                    }

                    Group={
                            "CH"
                            "NA"
                            "UJ"
                            "TW"
                    }

                    Group={
                            "BY"
                            "CC"
                            "DY"
                            "GP"
                            "JA"
                            "JU"
                            "KP"
                            "PJ"
```

```
                "SR"
                "TA"
                "YC"
                "YJ"
                "YY"
}
```

Appendix 5. Input file for Arlequin of *Anopheles sinensis* s.s. microsatellites

```
[Profile]
      Title="Anopheles sinensis ss population genetic structure in East Asia"
      NbSamples=23
      GenotypicData=1
      GameticPhase=0
      RecessiveData=0
      DataType=MICROSAT
      LocusSeparator=WHITESPACE
      MissingData='?'
      CompDistMatrix=1
[Data]
  [[Samples]]    #Data for 4Loci: SSR01 SSR02 SSR03 SSR04
      SampleName="Pop1"
      SampleSize=11
      SampleData=       {
        AD1_          1   236 234 289 213
                          246 248 289 215
        AD4_          1   246 234 291 213
                          248 234 293 213
        AD5_          1   246 248 291 211
                          248 250 291 213
        AD9_          1   248 234 289 211
                          248 234 291 211
        AD10_         1   240 232 289 213
                          248 232 291 215
        AD11_         1   246 244 289 215
                          246 252 289 219
        AD12_         1   248 248 285 213
                          248 250 289 215
        AD13_         1   248 242 289 213
                          248 246 293 213
        AD15_         1   238 234 289 213
                          248 234 289 215
        AD16_         1   234 234 289 213
                          234 248 289 215
        AD17_         1   246 234 289 215
                          248 234 291 215
      }
      SampleName="Pop2"
      SampleSize=16
      SampleData=       {
        BS1_          1   240 234 291 213
                          240 244 293 215
        BS3_          1   240 234 289 213
                          240 252 289 213
        BS4_          1   240 234 289 213
                          248 250 291 219
        BS5_          1   240 234 285 213
                          242 234 291 215
        BS6_          1   242 234 285 215
                          242 234 291 215
        BS9_          1   234 234 289 213
                          234 236 293 215
        BS10_         1   240 234 289 213
```

```
                240 248 291 213
  BS11_       1   236 248 289 213
                240 248 289 213
  BS12_       1   236 248 289 213
                242 248 291 215
  BS13_       1   240 234 289 215
                242 248 291 225
  BS17_       1   240 248 289 215
                242 248 291 215
  BS18_       1   234 248 291 213
                236 248 293 217
  BS19_       1   240 246 287 215
                240 248 289 215
  BS22_       1   240 240 291 213
                248 252 293 213
  BS24_       1   240 248 291 215
                240 250 291 215
  BS25_       1   240 248 289 213
                240 252 291 215
}
SampleName="Pop3"
SampleSize=8
SampleData=     {
  CC1_        1   234 250 289 213
                240 252 289 213
  CC2_        1   238 248 287 213
                242 250 289 215
  CC3_        1   236 248 289 215
                238 250 291 215
  CC4_        1   238 234 289 213
                238 234 291 215
  CC5_        1   236 246 289 213
                240 250 291 213
  CC11_       1   234 248 289 213
                240 254 289 213
  CC13_       1   240 248 283 219
                248 248 293 219
  CC15_       1   248 234 289 213
                248 234 291 215
}
SampleName="Pop4"
SampleSize=15
SampleData=     {
  DY1_        1   242 248 289 213
                248 248 291 213
  DY2_        1   240 244 289 213
                248 246 291 215
  DY3_        1   234 234 283 213
                236 234 291 213
  DY4_        1   236 248 291 211
                248 250 291 215
  DY5_        1   234 248 291 213
                242 254 291 215
  DY6_        1   234 248 291 227
                234 248 291 227
  DY8_        1   240 238 285 213
                242 248 291 215
  DY9_        1   234 236 289 211
                246 236 291 213
  DY11_       1   236 234 291 215
                248 246 291 215
```

```
   DY12_        1   234 246 291 215
                    234 246 291 215
   DY13_        1   248 234 289 215
                    248 252 291 215
   DY14_        1   238 234 289 213
                    238 252 291 213
   DY15_        1   234 234 287 211
                    236 242 289 223
   DY16_        1   234 234 291 211
                    248 240 291 213
   DY17_        1   248 244 291 213
                    248 254 291 213
}
SampleName="Pop5"
SampleSize=25
SampleData=       {
   ER1_         1   248 254 289 213
                    248 254 291 213
   ER2_         1   248 248 287 213
                    248 250 291 215
   ER3_         1   234 234 281 213
                    248 234 287 234
   ER4_         1   240 234 ? 211
                    248 242 ? 215
   ER5_         1   248 248 289 213
                    248 248 289 213
   ER6_         1   246 238 289 215
                    248 248 291 215
   ER7_         1   234 234 285 211
                    248 236 291 215
   ER8_         1   234 234 289 215
                    248 234 289 215
   ER10_        1   234 234 285 215
                    248 236 291 215
   ER11_        1   248 242 289 215
                    248 248 289 215
   ER12_        1   236 242 285 213
                    246 246 289 213
   ER13_        1   246 246 281 213
                    248 248 285 215
   ER14_        1   240 234 289 215
                    240 234 291 215
   ER15_        1   248 234 285 213
                    248 242 291 215
   ER16_        1   240 242 283 213
                    248 248 289 213
   ER17_        1   248 248 289 211
                    248 248 289 215
   ER19_        1   242 234 285 215
                    248 234 289 215
   ER21_        1   236 234 289 213
                    240 234 291 215
   ER22_        1   242 248 289 215
                    248 248 289 215
   ER25_        1   242 248 291 215
                    248 248 315 227
   ER26_        1   242 248 285 211
                    248 248 285 215
   ER28_        1   248 234 285 213
                    248 248 285 213
   ER29_        1   240 234 285 215
```

```
                248 234 289 215
  ER30_       1   234 234 287 213
                242 252 293 215
  ER31_       1   248 234 283 215
                248 234 285 217
}
SampleName="Pop6"
SampleSize=17
SampleData=       {
  GP1_        1   240 236 291 213
                240 246 291 215
  GP2_        1   242 234 291 213
                246 236 293 215
  GP3_        1   238 234 291 213
                242 234 291 215
  GP4_        1   236 234 291 213
                238 252 293 213
  GP5_        1   246 250 287 215
                248 250 291 215
  GP6_        1   238 234 289 213
                248 234 291 217
  GP7_        1   234 234 289 215
                248 248 291 215
  GP9_        1   242 238 281 203
                246 254 291 203
  GP10_       1   236 234 287 213
                246 234 291 215
  GP11_       1   238 234 291 213
                248 248 291 215
  GP12_       1   236 234 291 213
                246 246 291 215
  GP13_       1   236 234 291 215
                246 250 291 215
  GP14_       1   236 234 293 213
                242 252 293 215
  GP15_       1   234 236 291 213
                242 236 291 215
  GP16_       1   234 234 289 213
                236 248 291 213
  GP17_       1   238 240 289 215
                238 252 289 219
  GP18_       1   234 234 291 213
                240 248 291 215
}
SampleName="Pop7"
SampleSize=43
SampleData=       {
  GR1_        1   234 248 289 213
                234 248 289 215
  GR5_        1   236 248 289 215
                242 250 291 215
  GR6_        1   234 234 289 213
                248 248 289 215
  GR8_        1   248 234 289 215
                248 234 291 215
  GR11_       1   248 242 289 213
                248 250 291 215
  GR12_       1   240 236 289 215
                248 240 291 227
  GR13_       1   248 234 291 215
                248 234 291 217
```

GR14_ 1 236 234 293 215
248 234 293 215
GR15_ 1 236 234 289 213
244 242 291 215
GR18_ 1 234 250 285 213
248 250 287 219
GR19_ 1 248 248 289 213
248 248 289 215
GR20_ 1 236 242 285 213
248 242 291 219
GR21_ 1 246 240 289 211
248 252 291 215
GR23_ 1 246 250 289 211
248 250 291 219
GR24_ 1 238 242 289 213
238 248 291 213
GR27_ 1 246 244 291 213
246 252 291 215
GR29_ 1 248 240 291 211
248 252 291 217
GR30_ 1 248 248 289 215
248 250 291 229
GR31_ 1 234 234 289 213
248 234 289 215
GR32_ 1 248 250 231 213
248 250 289 213
GR33_ 1 248 248 285 215
248 248 289 215
GR34_ 1 238 236 289 213
248 252 291 215
GR35_ 1 234 248 289 217
248 252 291 227
GR36_ 1 238 234 291 215
248 248 293 215
GR37_ 1 234 240 285 215
238 240 291 219
GR38_ 1 248 250 289 215
248 252 291 215
GR39_ 1 234 234 289 213
248 242 291 215
GR40_ 1 234 254 285 213
248 254 291 215
GR41_ 1 242 242 291 215
248 248 291 215
GR42_ 1 248 234 289 213
248 248 291 215
GR43_ 1 242 248 293 219
248 252 293 227
GR44_ 1 248 234 289 211
248 234 289 217
GR45_ 1 246 234 291 211
248 234 293 219
GR46_ 1 240 240 289 213
244 240 289 217
GR47_ 1 248 234 285 ?
248 242 289 ?
GR48_ 1 248 246 287 213
248 248 293 215
GR49_ 1 234 248 289 213
240 248 289 215
GR50_ 1 248 236 281 213

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                248 248 289 215
  GR51_       1   248 234 283 213
                248 252 283 215
  GR52_       1   248 234 289 219
                248 250 291 219
  GR53_       1   248 248 289 213
                248 252 291 215
  GR54_       1   248 234 285 215
                248 250 289 215
  GR55_       1   248 234 289 215
                248 250 291 221
}
SampleName="Pop8"
SampleSize=11
SampleData=       {
  JA1_        1   236 236 289 215
                248 256 289 215
  JA4_        1   242 234 291 223
                242 248 291 229
  JA7_        1   236 234 229 213
                248 234 291 215
  JA8_        1   242 234 285 213
                248 242 287 215
  JA10_       1   234 234 291 213
                234 234 291 215
  JA12_       1   242 242 291 215
                248 244 291 217
  JA15_       1   238 234 287 213
                242 234 291 215
  JA16_       1   240 234 289 215
                248 248 293 217
  JA17_       1   242 234 289 219
                242 234 291 227
  JA18_       1   234 234 291 215
                236 252 291 215
  JA19_       1   234 252 291 213
                248 254 291 213
}
SampleName="Pop9"
SampleSize=29
SampleData=       {
  JI1_        1   236 248 285 215
                248 248 291 223
  JI2_        1   248 250 291 213
                248 252 291 215
  JI3_        1   248 242 289 213
                248 248 291 213
  JI4_        1   236 234 285 213
                248 248 289 215
  JI5_        1   240 246 285 211
                248 256 285 215
  JI6_        1   248 234 289 213
                248 252 291 215
  JI8_        1   234 234 289 215
                248 236 291 215
  JI9_        1   236 238 291 213
                248 238 291 213
  JI10_       1   236 248 289 213
                248 252 291 213
  JI12_       1   240 252 283 213
                248 252 283 215
```

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  JI13_        1   248 236 289 213
                   248 250 291 215
  JI14_        1   248 234 291 183
                   248 248 293 215
  JI15_        1   248 230 289 213
                   248 250 291 229
  JI16_        1   242 234 285 215
                   248 234 289 215
  JI17_        1   238 234 285 217
                   246 252 291 227
  JI18_        1   240 234 289 211
                   248 234 291 213
  JI20_        1   240 238 285 213
                   240 238 289 215
  JI22_        1   248 248 285 213
                   248 248 287 213
  JI24_        1   248 234 289 215
                   248 236 291 215
  JI25_        1   234 248 293 213
                   248 248 293 215
  JI26_        1   248 234 285 213
                   248 234 291 215
  JI27_        1   236 234 285 213
                   248 248 289 213
  JI28_        1   248 236 289 213
                   248 248 291 215
  JI29_        1   242 242 291 213
                   248 248 291 215
  JI30_        1   248 248 287 213
                   248 248 289 213
  JI31_        1   246 234 285 213
                   248 248 289 217
  JI32_        1   248 234 291 217
                   248 242 291 217
  JI33_        1   248 234 291 213
                   248 252 291 215
  JI34_        1   240 248 289 213
                   248 250 289 215
}
SampleName="Pop10"
SampleSize=10
SampleData=       {
  JU1_         1   234 234 289 215
                   236 252 291 215
  JU2_         1   248 246 291 215
                   248 252 291 219
  JU4_         1   242 236 289 213
                   248 238 291 213
  JU5_         1   236 248 291 215
                   240 248 291 215
  JU7_         1   240 236 219 213
                   240 236 219 213
  JU13_        1   234 248 281 215
                   240 250 289 217
  JU14_        1   240 234 285 211
                   248 248 287 215
  JU15_        1   248 252 289 213
                   248 252 289 213
  JU16_        1   242 234 291 213
                   248 234 291 215
  JU18_        1   248 234 289 213
```

```
                248 236 291 213
}
SampleName="Pop11"
SampleSize=14
SampleData=     {
  KP1_        1   236 234 287 213
                  248 236 289 213
  KP2_        1   238 248 287 213
                  244 248 289 213
  KP3_        1   240 234 289 215
                  242 236 291 215
  KP4_        1   238 234 287 213
                  238 250 291 215
  KP5_        1   236 258 289 213
                  248 258 291 217
  KP7_        1   238 234 281 213
                  240 246 289 215
  KP8_        1   234 234 289 213
                  234 248 291 213
  KP12_       1   234 234 291 213
                  238 248 291 213
  KP17_       1   234 234 291 211
                  240 240 291 213
  KP18_       1   236 234 287 215
                  236 234 291 215
  KP19_       1   234 234 289 213
                  234 236 289 213
  KP20_       1   236 234 281 213
                  238 234 291 213
  KP21_       1   234 234 287 213
                  234 248 287 213
  KP22_       1   234 240 289 213
                  234 252 291 219
}
SampleName="Pop12"
SampleSize=6
SampleData=     {
  MA1_        1   242 234 281 213
                  242 234 293 215
  MA2_        1   242 236 289 215
                  242 248 291 215
  MA3_        1   242 234 291 213
                  242 248 291 219
  MA4_        1   242 234 291 213
                  242 246 291 215
  MA5_        1   238 234 289 213
                  240 240 289 213
  MA6_        1   238 242 287 217
                  238 246 287 217
}
SampleName="Pop13"
SampleSize=28
SampleData=     {
  NA1_        1   238 234 281 215
                  242 234 291 215
  NA2_        1   238 244 291 213
                  248 244 317 213
  NA3_        1   240 246 289 213
                  242 248 291 213
  NA4_        1   240 248 291 215
                  248 252 293 217
```

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  NA5_          1   240 234 289 213
                    240 234 291 215
  NA6_          1   234 234 285 215
                    242 236 293 217
  NA7_          1   240 234 289 213
                    240 234 291 213
  NA9_          1   240 234 287 215
                    242 238 289 215
  NA10_         1   248 250 289 213
                    250 250 289 215
  NA12_         1   234 234 287 215
                    240 234 291 215
  NA13_         1   242 234 291 215
                    248 238 291 215
  NA14_         1   240 234 289 213
                    240 236 289 215
  NA15_         1   234 234 287 213
                    240 250 287 215
  NA16_         1   244 234 285 215
                    246 234 291 223
  NA17_         1   240 240 291 213
                    250 248 293 215
  NA18_         1   236 248 289 215
                    244 248 289 219
  NA19_         1   240 234 285 213
                    242 238 291 213
  NA20_         1   236 234 291 213
                    242 234 291 215
  NA21_         1   240 230 285 213
                    240 234 289 215
  NA22_         1   234 234 289 213
                    240 252 291 215
  NA23_         1   240 234 289 213
                    242 240 291 215
  NA24_         1   240 248 291 213
                    240 250 291 217
  NA25_         1   240 234 289 213
                    248 234 291 229
  NA26_         1   240 234 289 215
                    248 234 291 215
  NA27_         1   236 234 289 213
                    240 234 289 213
  NA28_         1   240 234 291 213
                    248 234 291 215
  NA29_         1   236 234 289 213
                    240 236 289 219
  NA30_         1   248 230 289 215
                    248 248 289 215
}
SampleName="Pop14"
SampleSize=16
SampleData=       {
  PJ4_          1   234 248 287 215
                    240 252 291 225
  PJ5_          1   234 234 291 215
                    234 242 291 215
  PJ8_          1   236 236 289 213
                    246 236 291 213
  PJ10_         1   238 248 289 213
                    240 248 291 219
  PJ12_         1   234 234 289 213
```

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                234 234 291 215
  PJ14_     1   236 234 287 213
                238 234 291 215
  PJ15_     1   240 246 289 213
                246 246 291 215
  PJ20_     1   234 234 291 213
                242 234 291 219
  PJ22_     1   234 236 289 215
                236 246 291 219
  PJ25_     1   242 234 289 213
                248 234 291 215
  PJ30_     1   240 234 289 215
                246 250 289 217
  PJ32_     1   234 234 291 213
                248 242 291 213
  PJ36_     1   234 234 289 211
                234 234 289 215
  PJ37_     1   242 236 291 215
                248 248 293 217
  PJ40_     1   234 234 289 209
                238 242 291 219
  PJ41_     1   234 234 291 213
                238 236 293 215
}
SampleName="Pop15"
SampleSize=24
SampleData=     {
  SR2_      1   240 248 291 213
                240 252 291 215
  SR3_      1   236 248 289 213
                242 250 291 215
  SR4_      1   234 234 281 213
                236 250 287 215
  SR7_      1   234 234 287 213
                240 248 289 213
  SR8_      1   234 248 289 213
                234 248 291 215
  SR10_     1   240 248 283 213
                248 250 289 215
  SR11_     1   234 234 291 213
                252 234 293 213
  SR12_     1   236 234 289 213
                240 248 291 215
  SR14_     1   234 244 287 213
                236 248 291 215
  SR15_     1   240 234 289 213
                240 252 291 217
  SR16_     1   234 236 291 213
                240 240 291 215
  SR18_     1   234 234 289 213
                236 248 291 217
  SR19_     1   236 234 291 211
                240 246 291 215
  SR20_     1   240 234 289 211
                240 234 291 213
  SR22_     1   238 236 291 215
                238 248 291 215
  SR23_     1   236 242 289 213
                240 246 291 215
  SR24_     1   242 250 293 217
                248 254 293 219
```

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  SR25_        1   240 234 291 213
                   248 252 291 215
  SR26_        1   240 242 287 213
                   242 254 291 227
  SR27_        1   236 240 289 215
                   248 240 289 215
  SR28_        1   236 248 291 213
                   238 248 291 215
  SR30_        1   232 248 289 213
                   236 248 291 215
  SR32_        1   234 234 289 213
                   246 234 291 215
  SR33_        1   240 248 291 213
                   244 248 295 227
}
SampleName="Pop16"
SampleSize=12
SampleData=      {
  TA1_         1   234 234 291 213
                   240 248 291 215
  TA2_         1   234 230 289 213
                   234 230 289 213
  TA3_         1   240 234 291 213
                   242 234 309 219
  TA4_         1   232 230 289 213
                   242 248 291 215
  TA7_         1   246 234 283 215
                   248 246 291 219
  TA11_        1   236 234 285 213
                   238 234 289 223
  TA12_        1   240 234 281 215
                   240 250 291 217
  TA13_        1   236 248 291 215
                   240 252 291 215
  TA14_        1   234 234 291 213
                   236 248 291 213
  TA16_        1   242 234 289 213
                   248 236 291 215
  TA17_        1   234 240 289 215
                   240 246 289 215
  TA18_        1   236 234 291 213
                   240 242 297 213
}
SampleName="Pop17"
SampleSize=16
SampleData=      {
  UJ1_         1   236 234 291 211
                   248 234 293 213
  UJ2_         1   236 234 291 213
                   240 240 291 215
  UJ3_         1   236 234 289 213
                   240 248 291 215
  UJ5_         1   236 234 285 215
                   242 242 289 215
  UJ6_         1   234 234 289 215
                   248 248 291 215
  UJ7_         1   238 248 287 213
                   242 252 289 227
  UJ8_         1   234 248 291 213
                   242 254 291 215
  UJ9_         1   238 234 285 213
```

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                248 248 287 215
  UJ11_       1   234 250 287 213
                234 250 289 213
  UJ12_       1   240 248 281 213
                248 260 291 213
  UJ13_       1   240 234 289 213
                242 234 289 213
  UJ14_       1   234 234 289 215
                236 248 291 219
  UJ15_       1   244 234 289 213
                248 248 291 213
  UJ16_       1   234 248 289 213
                240 252 291 219
  UJ17_       1   240 248 289 215
                248 248 291 215
  UJ18_       1   240 234 291 213
                248 250 295 215
}
SampleName="Pop18"
SampleSize=9
SampleData=     {
  YC23_       1   236 240 287 213
                242 248 289 215
  YC25_       1   236 234 289 213
                236 234 289 215
  YC28_       1   236 248 289 213
                242 248 291 215
  YC31_       1   232 230 289 213
                240 230 293 227
  YC36_       1   236 232 291 213
                248 234 291 215
  YC39_       1   236 236 289 215
                248 242 291 215
  YC41_       1   236 240 289 213
                248 250 291 213
  YC42_       1   232 234 287 211
                236 248 291 213
  YC43_       1   238 234 289 213
                240 234 289 213
}
SampleName="Pop19"
SampleSize=11
SampleData=     {
  YJ6_        1   238 248 291 213
                242 248 291 215
  YJ9_        1   236 236 289 213
                242 248 289 219
  YJ10_       1   240 234 291 213
                248 248 291 213
  YJ11_       1   240 234 283 213
                240 246 291 213
  YJ13_       1   236 244 289 213
                248 250 291 215
  YJ22_       1   248 246 287 213
                248 248 291 215
  YJ29_       1   238 234 291 213
                248 236 303 213
  YJ34_       1   240 240 289 213
                248 250 291 213
  YJ2_        1   234 242 291 201
                234 248 291 213
```

```
  YJ4_          1   234 234 291 213
                    240 252 291 215
  YJ5_          1   234 236 291 215
                    242 256 291 215
}
SampleName="Pop20"
SampleSize=4
SampleData=       {
  YY11_         1   238 236 289 213
                    238 236 291 213
  YY21_         1   240 234 287 213
                    240 250 289 213
  YY28_         1   234 232 291 213
                    240 232 291 215
  YY42_         1   240 234 285 213
                    240 248 289 227
}
SampleName="Pop21"
SampleSize=16
SampleData=       {
  BA1_          1   234 234 289 213
                    240 248 291 219
  BA2_          1   232 230 291 215
                    232 230 291 215
  BA3_          1   236 234 289 213
                    244 248 291 215
  BA4_          1   232 230 287 213
                    234 236 289 215
  BA5_          1   248 234 291 213
                    248 252 291 215
  BA9_          1   234 230 291 213
                    240 248 291 215
  BA12_         1   238 234 291 213
                    248 242 291 213
  BA16_         1   232 230 291 215
                    238 246 291 215
  BA17_         1   232 230 289 213
                    248 230 291 215
  BA18_         1   232 230 283 215
                    232 230 289 215
  BA19_         1   236 234 291 213
                    242 242 291 215
  BA20_         1   232 230 291 213
                    238 230 291 213
  BA21_         1   234 248 291 213
                    234 250 293 215
  BA22_         1   232 230 289 211
                    248 248 291 215
  BA23_         1   234 234 289 211
                    242 234 291 213
  BA24_         1   240 234 289 213
                    248 234 289 213
}
SampleName="Pop22"
SampleSize=13
SampleData=       {
  CH001_        1   236 236 291 213
                    236 240 291 215
  CH002_        1   236 234 291 213
                    236 238 291 213
  CH004_        1   ? 234 297 213
```

```
                ? 234 307 213
  CH005_    1   234 234 291 211
                236 238 291 215
  CH006_    1   ? 234 291 213
                ? 234 291 215
  CH007_    1   ? 240 234 289
                ? 240 234 289
  CH008_    1   236 234 287 213
                240 234 289 215
  CH009_    1   236 234 289 213
                238 240 289 217
  CH010_    1   240 234 291 213
                240 236 291 217
  CH011_    1   240 234 291 213
                240 234 291 213
  CH012_    1   236 234 291 213
                240 234 293 215
  CH013_    1   234 236 287 213
                236 236 298 213
  CH014_    1   238 234 291 213
                240 239 291 215
}
SampleName="Pop23"
SampleSize=20
SampleData=     {
  TW001_    1   238 234 290 213
                238 248 290 213
  TW002_    1   236 234 287 213
                236 240 291 215
  TW003_    1   240 244 293 219
                240 244 293 219
  TW004_    1   234 234 281 213
                234 234 298 215
  TW005_    1   232 234 291 203
                236 246 291 215
  TW006_    1   236 234 283 213
                240 244 291 213
  TW007_    1   236 240 291 215
                240 242 291 217
  TW008_    1   238 234 291 213
                238 244 291 217
  TW009_    1   236 234 291 213
                238 238 291 213
  TW010_    1   233 234 291 213
                236 234 291 215
  TW011_    1   236 240 293 213
                240 240 297 213
  TW012_    1   233 242 291 215
                238 242 295 219
  TW013_    1   238 234 295 213
                240 234 297 215
  TW014_    1   234 234 283 213
                236 248 297 217
  TW015_    1   236 234 287 213
                242 236 297 215
  TW016_    1   238 244 283 213
                238 244 287 215
  TW017_    1   233 242 291 213
                238 242 291 213
  TW018_    1   234 ? 287 213
                240 ? 293 215
```

```
  TW019_      1   238 244 291 215
                  238 244 291 221
  TW020_      1   238 244 283 213
                  240 248 297 215
}
```

감사의 글

저에게 연구할 수 있는 기회를 주시고, 자연과학도로서의 자세를 가르쳐주신 김원 선생님 감사 드립니다. 이화여자대학교 정종우 교수님의 가르침이 없었다면 여기까지 절대 올 수 없었을 것이라 생각합니다. 깊은 감사 드리며 앞으로도 정진하는 모습 보여드리도록 노력하겠습니다. 부족한 저의 학위 논문을 심사해 주시고, 더욱 좋은 논문이 될 수 있도록 조언해주신 심사위원장님과 심사위원님들께 감사 드립니다. 진화학과 유전학의 학문적 즐거움을 처음 가르쳐주신 성신여자대학교 김진일 교수님과 박경숙 교수님 감사 드립니다. 말라리아 매개 모기 표본을 제공해주시고, 조언을 아끼지 않으신 연세대학교 이한일 교수님 감사 드립니다.

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